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NOTE

BOOK REVIEWS

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REPRODUCTIVE BIOLOGY OF THE CARRION-FLOWER, *SMILAX HERBACEA* (SMILACACEAE)

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ABSTRACT. Pollination biology, reproductive output, and population structure of male and female plants and flowers of *Smilax herbacea* were studied in nearly 900 individuals from 11 roadside populations in northeast-central Connecticut over a three-year period. Percentages of either sex did not vary across sites or between years. Reproductive plants represented 60% of an average population and nearly 65% of these were male. Female mortality is suggested as the most likely reason for the strong male bias (2.3♂:1♀). The male plants, although smaller, had twice the number of inflorescences, and 68% more flowers than female plants. Both inflorescence and flower number were significantly correlated with plant size in male plants. This correlation was absent for female plants implying that male plants are less constrained in the number of inflorescences and flowers they can produce. Although site size, population size, and population density of both female and male plants varied significantly across sites, gender and overall plant densities were not correlated with site size. However, a significant interaction was found between the densities of each sex and the site of their occurrence, suggesting that distribution of gender patterns may be influenced by site-specific ecological factors. *Smilax herbacea* can be characterized as a generalist in its attraction of pollinators. The carrion-like odor produced in tepals of male and female flowers, and the pollen reward of the staminate flowers attract bees, beetles, and flies. Due primarily to their high mobility and good pollen carrying capacity, andrenid and halictid bees and anthomyiid and stratiomyiid flies are considered major pollinators. Minor pollinators include soldier (Cantharidae), long-horned (Cerambycidae), and fire-colored (Pyrochroidae) beetles. Overall fruit set was lower in 1995 than in 1994 or 1996; this likely was due to unusually wet conditions that year. No significant difference in fruit set among populations was detected. Less than 1% of intrapopulational fruit set variation was explained by either site size or by plant density. Male plant densities were not significantly correlated with fruit set across sites. Furthermore, experimental interpopulational crosses did not significantly increase fruit set. These facts imply resource rather than pollen limitation in female plants.

Key Words: *Smilax herbacea,* dioecy, sex ratio, pollination mechanisms, entomophily, fruit set, pollen limitation, resource limitation

The genus *Smilax* L. comprises about 200 tropical and temperate species all of which are dioecious lianas, scramblers, or herbs. Species of *Smilax* have long been recognized as insect pollinated (Delpino 1880), and were grouped by Lovell (1920) with green flowered species pollinated by flies, beetles, and small bees. Honeybee visitation to some species was observed by Pellet (1976). For *S. rotundifolia,* Kevan et al. (1991) recorded visits from a *Bombus* sp. and mosquitoes. Nothing further has been reported regarding the pollination biology in the genus. This study was undertaken to better understand the reproductive biology and the mechanisms of pollination in dioecious *S. herbacea,* and to test hypotheses regarding the adaptive significance of flower form and function.

Smilax herbacea L., distributed from southeastern Canada south to Georgia and west to Manitoba and Missouri, is an herbaceous, perennial geophyte sprouting an annual shoot system from a short, thickened rhizome. Plants occur most commonly along roadsides, but also in meadows, at forest edges, or within forests. The shoot system may be branched, and may extend to a length of close to three meters. Plants remain erect for at least a portion of their length, then become scandent. Shoots attach to neighboring vegetation by paired, stipular tendrils. This species is dioecious. It has been suggested that sex in *S. herbacea* is determined by X and Y chromosomes (Mangaly 1968) among the n = 13 chromosomes (Lindsay 1930). Plants of *S. herbacea* flower in Connecticut during the last week in May through the first three weeks in June, the fruit maturing in September. Inflorescences occur as orbicular, pedicellate umbels on long, axillary peduncles either on primary axes or, less often, on lateral branches (Figure 1). The inflorescences are conspicuous and odoriferous. Flowers average 8–10 mm in diameter and bear six green tepals with glandular papillae along their margins (Pennell 1916). Further, the common name is appropriate, and the carrion-like odor released by the flowers of *S. herbacea* led us to suspect saprocantharophily or sapromyophily (Faegri and van der Pijl 1979). Staminate flowers bear six stamens with undifferentiated, bilocular anthers. Both the anthers and their copious pollen are white to yellow-white. Pistillate flowers bear conspicuous, green ovaries with greenish-white stigma lobes. Filament remnants are obvious at the base of the ovary. The advertising of a pollen reward by the yellowish-white anthers in males is mimicked in female flowers by the relatively large stigma lobes.

Figure 1. *Smilax herbacea.* A. Stem segment of mature male plant—9/16 actual size. B. Staminate flower. C. Pistillate flower. Bars = 1 mm.

MATERIALS AND METHODS

Population demographics. Eight hundred sixty-nine individual plants were observed in 11 roadside populations in northeast-central Connecticut from May through June and from late August through September during 1994 and 1995. Additionally, fruit set was assayed in 1996. Representative vouchers are deposited in the University of Connecticut herbarium (CONN). Roadside populations were selected because they were the only sites where flowering individuals occurred. For this study, populations were defined as localized concentrations of plants with at least one female plant present. The plants within each of the populations were never more than nine meters from their nearest neighbor. The presence of a female plant allowed intrapopulational crosses and interpopulational fruit set comparisons. Plants in all populations grew within three meters of a road. Site perimeters were arbitrarily determined by the plants at the periphery of a population. All populations bordered areas where *Smilax* plants were absent, viz., forests, fields, or dwellings. In all cases, the peripheral plants defining the boundary of a given site were a minimum of 500 meters from any other plants. Because flowering individuals occurred in disturbed, roadside populations, some plants marked over a two-year period were lost to summer mowing. Data for site size, number of individuals per population, and plant density were compiled from observations of six 1994 populations and of ten 1995 populations, five new for that year. One 1994 site was lost to mowing. Individual sites were mapped, plants were counted, and site size (m^2) was determined. Using these data, plant densities (plants per 1000 m^2) were calculated. Population demographics were further investigated by recording the number of individuals per population and scoring individuals as female, male, or nonreproductive. Because *S. herbacea* is not clonal, individuals were easily identified. Sex ratios were determined and compared among populations using the G-test (Sokal and Rohlf 1995). The size of male and female plants was determined by measuring the length of primary stems at anthesis.

To investigate the relationships between site size and plant density (all individuals, or males, or females) and between site size and reproductive output (mature fruit set), tests for correlations were conducted. Tests for correlations were also conducted between fruit set per site and plant density per site. To determine whether the density of pollen donors within a site had an effect on fruit set, a correlation was looked for between mean fruit set and the density of male plants across sites. To determine if sex expression was independent of site, a Chi-square test of independence was performed using the frequencies of male, female, and nonreproductive plants for each of the ten 1995 sites.

Staminate and pistillate flower demographics, morphology, and phenology. The number of inflorescences per plant was determined for all members of each population. The number of flowers per inflorescence was determined from randomly selected male and female plants from each population. Relationships between either flower number or inflorescence number and the size of the plants, measured as the length of primary shoots, were investigated by regressing flower number on inflorescence number and inflorescence and flower number on plant size.

The morphology of staminate and pistillate flowers was investigated and compared across populations. Both dried and alcohol-preserved voucher specimens were collected. Perianth diameters of 50 pistillate flowers from five populations and 50 staminate flowers from six populations were measured in the laboratory using alcohol-preserved specimens. These measurements were compared using a two-way ANOVA.

Study of flowering phenology involved random selection and marking with acrylic paint of 55 staminate flowers and 52 pistillate flowers from among 30 inflorescences (from which insects were excluded), three from each 1995 population. The maturation of marked flowers was recorded twice each day, early morning and late afternoon, until senescence. Stigmas were considered receptive while color, size, and appearance remained constant. Loss of receptivity was indicated by a darkening of the stigmatic surface accompanied by shrinkage of the stigma lobes and/or loss of tepals. Longitudinal sections of fresh flowers were made to determine the presence or absence of nectaries.

Pollination biology. Faegri and van der Pijl (1979) established criteria that allow discrimination of pollinators from scavengers. First, a relationship must exist between the flower and the pollinator that contributes to regular pollination, i.e., an attractant or reward must be present. Second, the body of the pollinator should mechanically promote pollen adherence allowing for effective pollen dispersal. Finally, the pollinator should demonstrate a high frequency of flower visits, thus requiring at least moderate mobility. Baker et al. (1971) suggested that major and minor pollinators might be distinguished by their degree of mobility, assuming more pollen will be moved around by more mobile visitors. Floral visitors were evaluated as potential pollinators based on these four criteria. In order to obtain a quantitative estimate of pollinator activity, 50 inflorescences, 25 for each sex, from seven populations were observed and assessed during 10-minute intervals for the frequency of visitation and movement patterns. Insect visitors were surveyed for the presence or absence of pollen grains. If pollen was present, a pollen sample was removed and examined for grains of *Smilax herbacea.* Flower visitors were either collected for identification or noted (when identity known) whenever they were observed on flowers. Voucher specimens of all insect visitors have been deposited in the University of Connecticut insect collection.

Reproductive output. The number of fruits matured per infructescence and the percent fruit set were determined for randomly selected infructescences during 1994 and 1995. Because fruit set data for the 1995 season displayed adverse effects, presumably caused by unusually wet weather conditions, 1996 fruit set data from 12 populations were included. Three populations were new for that year. Pedicel scars on the infructescence axis gave a precise indication of the number of flowers produced; thus, it was not necessary to count flowers prior to counting fruits to determine fruit set. To account for possible loss to birds, green fruits were counted and subsequently followed to maturity. In 1994, fruit weight, the number of seeds per fruit, and weights of seeds were determined by sampling ripe fruit. Weights and counts of seeds were determined by separating the seeds from the fruit, counting the number of seeds per fruit, cleaning the seed by hand, air drying the seeds at ambient temperatures for one week, recleaning, and weighing.

Crosses were performed artificially by touching the pollen-containing anthers of staminate flowers to the stigmatic surface of pistillate flowers in inflorescences that had been bagged prior to hand pollination. All bags used in these experiments were constructed from white, nylon insect netting with a 1 mm × 0.75 mm mesh. To ensure stigmas were receptive, pollinations were performed within 48 hours of flower opening. Fruit set resulting from these crosses was compared with that of controls. Both interpopulation and intrapopulation crosses were performed. Analyses of variance tests were performed within and among populations to detect patterns of variation in fruit set.

RESULTS

Population demographics. Site size varied greatly, from 50 to 1045 m^2 (Table 1). Populations consisted of from 16 to 254

Table 1. Population size, numbers of individuals by sex, and sex ratios for eleven 1994 and 1995 sites. * $P < 0.5$, ** $P < 0.01$.

Population	Size (m^2)	Year	Number of Individuals	Males		Females		Nonflowering		Hermaphrodites		Ratio	G Statistics
				#	%	#	%	#	%	#	%		
Bolton Road	450	1994	—	—	—	—	—	—	—	—		—	—
		1995	30	14	46.7%	6	20%	10	33.3%	—	—	2.3:1	0.00
Cedar Swamp Road	550	1994	—	—	—	—	—	—	—	—	—	—	—
		1995	254	131	51.6%	39	15.3%	84	33.1%	—	—	3.5:1	4.25*
Bone Mill Road	225	1994	26	6	23.1%	5	19.2%	15	57.7%	—	—	1.2:1	1.16
		1995	16	5	31.3%	7	43.7%	4	25%	—	—	0.7:1	4.12*
South Eagleville Road	170	1994	—	—	—	—	—	—	—	—	—	—	—
		1995	41	16	39%	13	31.7%	11	26.8%	1	2.5%	1.2:1	2.83
Agronomy Farm	165	1994	52	27	51.9%	8	15.4%	17	32.7%	—	—	3.5:1	0.90
		1995	54	33	61.1%	3	5.6%	18	33.3%	—	—	10.2:1	10.11**
Knowlton Hill Road	1045	1994	—	—	—	—	—	—	—	—	—	—	—
		1995	134	52	38.8%	34	25.4%	47	35.1%	1	0.7%	1.6:1	3.54
Wormwood Site	185	1994	—	—	—	—	—	—	—	—	—	—	—
		1995	58	16	27.6%	3	5.2%	39	67.2%	—	—	5.6:1	2.06
Daleville Road North	185	1994	39	17	43.6%	10	25.6%	12	30.8%	—	—	1.7:1	0.61
		1995	46	20	43.5%	10	21.7%	16	34.8%	—	—	1.9:1	0.16
Daleville Road South	50	1994	26	14	53.8%	6	23.1%	6	23.1%	—	—	2.3:1	0.00
		1995	28	4	14.3%	5	17.8%	19	67.9%	—	—	0.8:1	2.53
Cary Tract	210	1994	23	12	52.2%	7	30.4%	4	17.4%	—	—	1.7:1	0.41
		1995	23	8	34.8%	5	21.7%	10	43.5%	—	—	1.6:1	0.42
Gurleyville Road	120	1994	19	6	31.6%	3	15.8%	10	52.6%	—	—	2:1	0.05
		1995	—	—	—	—	—	—	—	—	—	—	—
All sites	3355	1994	185	82	44.3%	39	21.1%	64	34.6%	—	—	2.1:1	—
		1995	684	299	43.7%	125	18.3%	258	37.7%	2	0.3%	2.4:1	—
		Both years	869	381	43.8%	164	18.9%	322	37.1%	2	0.2%	2.3:1	14.66

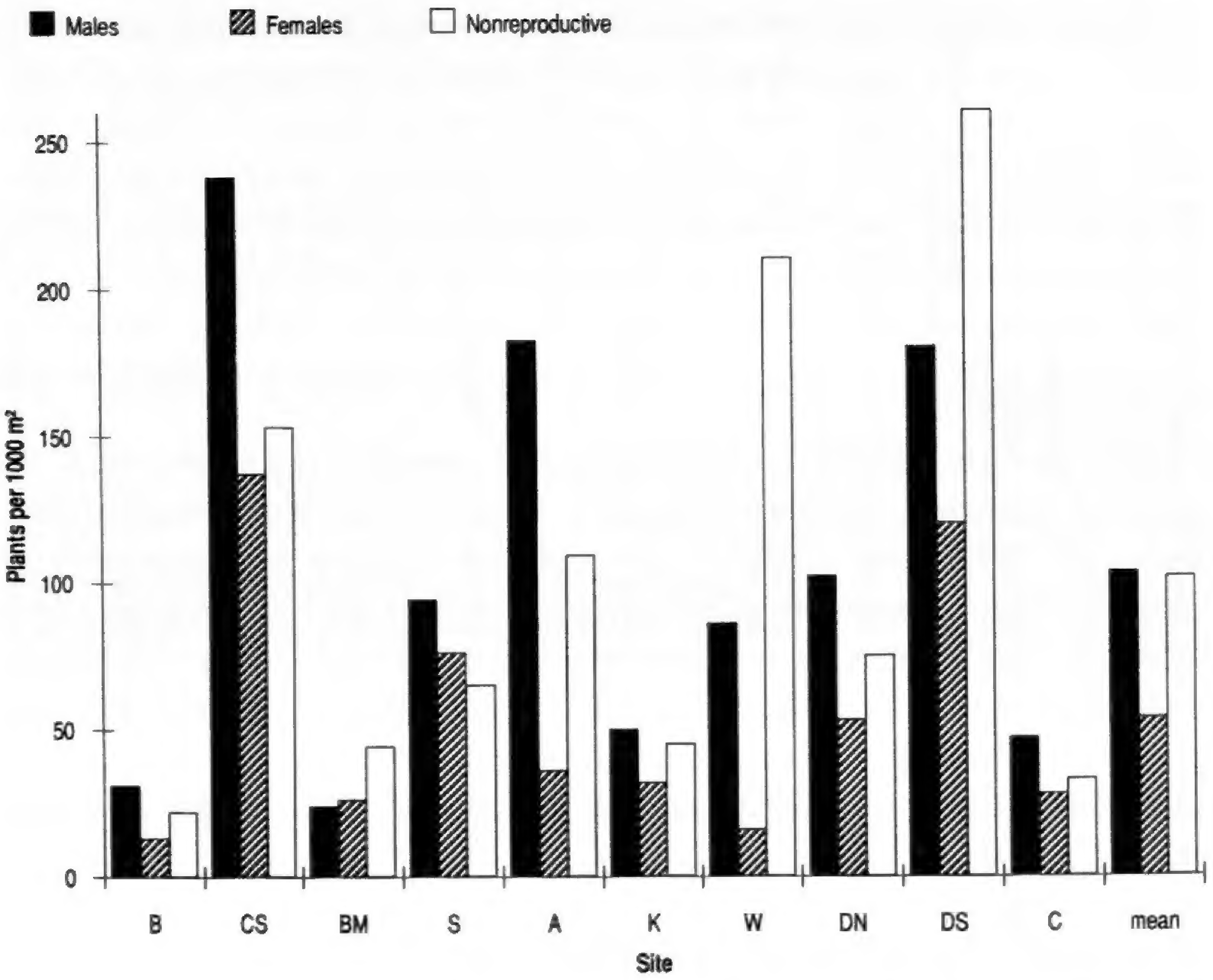

Figure 2. Comparison of mean population densities (plants per 1000 m^2) for male, female, and nonreproductive plants in ten 1995 populations. (B = Bolton Rd., CS = Cedar Swamp Rd., BM = Bone Mill Rd., S = S. Eagleville Rd., A = Agronomy Farm, K = Knowlton Hill Rd., W = Wormwood Site, DN = Daleville N. Rd., DS = Daleville S. Rd., C = Cary Tract)

individuals (mean per population = 54; Table 1). Staminate and pistillate plant densities also varied greatly from site to site (Figure 2). Neither male, female, nor overall plant densities were significantly correlated with site size (♂, r = 0.040, n = 10; ♀, r = 0.060, n = 10; overall, r = 0.305, n = 10, respectively). However, a Chi-square test for independence using frequencies of male, female, and nonreproductive plants across all ten 1995 populations showed a highly significant interaction between individual sites and gender densities among sites ($X^2 = 250.88$, 18 df, $P < 0.001$).

The mean percentages of plants of each sex from all sites for both years were as follows: ♂'s = 44%, ♀'s = 19% (Table 1). This gives a male biased sex ratio of 2.3♂:1♀. Significant heterogeneity in sex ratios was detected among sites, and three sites varied significantly from the 2.3♂:1♀ ratio. Further, although in-

Table 2. Mean number of inflorescences per plant among reproductive individuals in eleven 1994 and 1995 populations.

Population	Year	Males	Females	Hermaphrodites
Bolton Road	1995	12.1	2.8	—
Cedar Swamp Road	1995	14.4	6	—
Bone Mill Road	1994	29.4	6.4	—
	1995	26	17.8	—
South Eagleville Road	1995	22.7	4.9	14
Agronomy Farm	1994	14	7.1	—
	1995	18.6	12.3	—
Knowlton Hill Road	1995	19.3	5	5
Wormwood Site	1995	9.1	5.3	—
Daleville Road North	1994	15.3	10.5	—
	1995	16.9	5.9	—
Daleville Road South	1994	10.1	3.2	—
	1995	4.5	2	—
Cary Tract	1994	10	4.1	—
	1995	11	5	—
Gurleyville Road	1994	7	7	—
All sites	1994	14.8	6.4	—
	1995	15.5	6.7	9.5
	Both years	15.1	6.5	4.7

dividual populations showed marked differences in sex ratios between years, an analysis of variance performed on arcsine transformed data showed that neither the percentage of males nor the percentage of females varied significantly between years across all populations ($F = 0.328$, $df = 15$, $P = 0.576$, for males; $F = 0.107$, $df = 15$, $P = 0.748$, for females).

The mean length of the primary stems was 109 cm for male plants and 164 cm for female plants. Analysis of variance indicated that these differences were significant ($F = 8.12$, $df = 32$, $P < 0.01$).

Staminate and pistillate flower demographics, morphology, and phenology. Plants of both sexes varied greatly in the number of both inflorescences and flowers. The mean number of inflorescences per staminate plant was 15 (Table 2; range = 1–60), and each inflorescence bore an average of 30 flowers (range = 4–100). This is contrasted with female plants that averaged 6.5 inflorescences per plant (Table 2; range = 2–28) and averaged 41 flowers per inflorescence (range = 12–110). When all sites were considered for both years, male plants bore significantly more inflorescences than female plants ($F = 19.77$, $df = 31$, $P < 0.001$). When both flower number and inflorescence number were considered, male plants (average of 590 flowers/plant; Table 3) produced 68% more flowers than female plants (average of 351 flowers/plant; Table 3). Males showed greater variation in the number of inflorescences produced per plant than females ($r^2 = 44.5$, $n = 214$ for ♂'s; $r^2 = 31.8$, $n = 116$ for ♀'s). Flower numbers per inflorescence also varied greatly in both sexes (Table 3). Flower number per inflorescence consistently decreased with distance from the base along the primary axis. This is reflected in a highly significant negative correlation between the number of flowers in an inflorescence and the distance in cm of that inflorescence from the base ($r = 0.957$, $n = 29$, $P < 0.001$). Plants producing fewer inflorescences were likely to exhibit relatively less variation in flower number per inflorescence. Consequently, variation in flower number per inflorescence was more likely to be detected in plants producing many inflorescences, i.e., in male plants.

Little of the variation in either inflorescence or flower number was explained by plant height when plants were compared without regard to sex ($r^2 = 0.118$, $P = 0.0628$; $r^2 = 0.2182$, $P = 0.0053$ for inflorescence and flower number, respectively). However, when male and female plants were considered separately, much of the variation both in flower number ($r^2 = 0.755$, $P = 0.0014$) and inflorescence number ($r^2 = 0.6858$, $P < 0.0001$) was explained by plant height in male plants, whereas very little of the variation either in flower number ($r^2 = 0.009$, $P = 0.3113$) or inflorescence number ($r^2 = 0.0947$, $P = 0.3573$) was explained by plant height in female plants.

The diameter of the pistillate perianth averaged 8.0 mm (range = 5.9–9.3 mm). The mean diameter of staminate perianths was 10.1 mm (range = 6.9–12.5 mm). Although staminate flowers tended to be larger in diameter than pistillate flowers, a two-way ANOVA detected neither a significant difference in the variance between the sexes ($F = 1.081$, $df = 1$, $P > 0.75$) nor an added variance component due to population ($F = 0.053$, $df = 4$, $P > 0.75$).

Male plants typically inaugurated the reproductive season by flowering one to several days earlier than female plants. Many other differences were observed between staminate and pistillate

Table 3. Individual samples of plant height and flower production from six 1994 populations. * Numbers identify plants in specific populations: G = Gurleyville Road, C = Cary Tract, DS = Daleville Road South, DN = Daleville Road North, A = Agronomy Farm, B = Bone Mill Road.

Plant ID*	Height (cm)	Flowers/ Inflorescence	Inflorescences/ Plant	Total Number of Flowers/Plant
Female Plants				
G5	186	43	10	430
C12	237	42.1	7	295
C17	198	28.7	6	172
DS12	74	24.5	2	49
DS17	121	22.7	3	68
DS18	142	46.6	5	233
DS20	115	14	3	42
DN11	250	68.3	6	410
DN12	271	33	4	132
DN13	274	43.8	6	263
DN14	274	42	5	210
A37	236	68.2	27	1841
B1	173	66.3	10	663
B15	167	25.5	4	102
Mean	194	40.6	7.0	351
Male plants				
G3	144	42.8	23	939
G7	77	16.8	6	101
G8	75	7	5	35
G14	86	27.7	13	333
C5	167	24.6	5	123
C11	148	26.8	20	536
DS10	73	24	4	96
DS14	101	21.4	13	278
DS15	147	42.4	32	1357
DS19	88	28.5	4	114
DN5	157	33.5	24	805
DN17	141	25.3	12	304
DN23	244	45.2	34	1537
A13	100	14.4	7	101
A17	102	16.3	14	228
A20	67	16.2	5	81
A23	205	38.1	30	1144
B6	124	42.5	13	552
B12	175	48.1	14	673
B17	265	61.6	40	2465
Mean	134	30.2	15.9	590

flower maturation and between patterns of pollen availability and stigma receptivity. Staminate flowers consistently matured in a centripetal pattern, whereas flowers in female inflorescences did not exhibit any recognizable maturation pattern. Anthers dehisced well after the odor-producing tepals had reflexed, whereas stigmas were receptive the moment pistillate flowers opened. Due to pollen collection by pollinators and continual pollen predation by beetles, pollen was available in any given staminate flower for about one day, whereas pistillate flowers had receptive stigmas for three to four days. When simultaneously flowering staminate vs. pistillate flowers were compared, stigma receptivity consistently outlasted the pollen release of anthers. In addition, within an inflorescence many more pistillate flowers matured per day than did staminate flowers. When the overall means of individual staminate and pistillate inflorescence life spans (life span measured as the duration of pollen availability in a given staminate inflorescence, or the duration of stigma receptivity in a given pistillate inflorescence) were compared, no significant difference was detected (mean = 6.6 days for 114 staminate inflorescences [3138 flowers] in four plants; mean = 6.9 days for 38 pistillate inflorescences [2222 flowers] in four plants; $t = 2.447$, $P > 0.2$).

Pollination. Tepals in both male and female flowers of *Smilax herbacea* are green and were observed to secrete a liquid through glandular, epidermal papillae along the margins and at the apices of the tepals. This liquid is ignored by insect visitors. These compounds presumably are those responsible for the carrion-like odor, for when the tepals are removed, no odor is apparent. Based on observations of sectioned ovaries, there is no anatomical evidence for nectar production.

The pollen grains of *Smilax herbacea* do not contain viscin threads as Kevan et al. (1991) reported for *S. rotundifolia,* but are distinctly spinose with a very sticky pollenkitt. Pollen was moved from male to female flowers by insects. Of all the observed floral visitors, 89% were coleopteran, 4% were hymenopteran, and 7% were dipteran (Table 4). False darkling beetles (Scraptiidae, genus *Anaspis*) constituted 74% of the individual observations among coleopteran visitors and 66% of all visitors. These tiny beetles, however, lack hairs or other means of pollen dispersal and are sedentary, breeding on both female and male flowers and only occasionally feeding on the pollen of male flowers. Soldier beetles (Cantharidae) accounted for 13% of all beetles observed, long-horned beetles (Cerambycidae) for 5%, and fire-colored beetles (Pyrochroidae) for 4%. Species in these three families are moderately mobile (see below) and possess hairs and body parts to which pollen adheres. Click beetles (Elateridae) accounted for the remaining 1% of beetle observations. Click beetles have smooth body parts and lack hairs. No pollen was found on these beetles. Hymenopteran visitors consisted of two species of halictid bees and one species of andrenid bee. All these bees have hairy bodies, and large amounts of pollen were present on all individuals. These bees are also highly mobile. Of the four families of dipteran visitors, only the small scavenger flies (Anthomyiidae) and the large soldier flies (Stratiomyiidae) were found to carry pollen (Table 4). Both of these flies were highly mobile, possessing hairs on their legs and bodies among which large amounts of pollen were found. However, these flies accounted for only 1% of all observations.

Using the criteria given in the methods, floral visitors were evaluated as possible effective pollinators: beetles accounted for 80% of the possible pollinator frequency, bees for 13%, and flies for 7% (Table 4). Although accounting for only 20% of possible pollinators, small halictid and andrenid bees and anthomyiid and stratiomyiid flies were observed to be strikingly more mobile when contrasted with the relatively sedentary beetles. Insect visits were recorded for 20 of the 25 male inflorescences observed, but for only seven of the 25 female inflorescences. Beetles carrying *Smilax herbacea* pollen (cantharids, cerambycids, pyrochroids) were nearly immobile, spending at least 75 seconds on a single flower and often much longer. Further, beetles remained within the same inflorescence during the entirety of each 10 minute observation interval (Figure 3). Beetles were seldom observed visiting female inflorescences. Bees and flies, on the other hand, spent 16 seconds or less (flies = 16 seconds maximum, bees = 9 seconds maximum) on a single flower and 32 seconds or less (flies = 32 seconds maximum, bees = 19 seconds maximum) within a single inflorescence (Figure 3). Without exception, bees and flies visited many more flowers and plants of both sexes than beetles within each observation interval. Individual flies visited a minimum of nine flowers on four inflorescences of a single plant during an 82-second interval before moving to another plant. Individual bees visited a minimum of 10 flowers on six inflores-

Table 4. Frequency of insect visitors based on results of 27 ten-minute observation intervals. Families in bold have members considered likely pollinators. [a] The frequency of each visitor is expressed as the number and percentage of all observations.

Order	Family	Genus	Frequency of All Visitors[a]	Pollen Carriers (% of all individuals)
Coleoptera				80%
	Scraptiidae			
		Anaspis	160 66%	—
	Cantharidae			
		Podabrus	31 13%	46%
		Cantharis	1 —	1%
	Cerambycidae			
		Anoplodera	12 5%	18%
	Pyrochroidae			
		Pedilus	10 4%	15%
	Elateridae		2 1%	—
Hymenoptera				13%
	Halictidae		7 3%	10%
	Andrenidae		2 1%	3%
Diptera				7%
	Anthomyiidae		3 1%	4%
	Muscidae		12 5%	—
	Stratiomyiidae		2 1%	3%

cences on the same plant during a 52-second interval before moving to another plant. No differences were detected in the timing of bee and fly visitations between male and female flowers or inflorescences.

Reproductive output. All inflorescences (n = 10) that remained bagged for the duration of flowering showed 0% fruit set. Overall matured fruit set in open-pollinated controls, although quite variable, was lower in 1995 (53% from 9 sites) than in 1994 (69% from 6 sites; Table 5) or 1996 (73% from 12 sites; Table 5). The 1995 season was unusually wet and many infructescences succumbed to mildew, thus lowering fruit set potential for that year. Analyses of variance performed on arcsine transformed data revealed significant differences between fruit set in 1995 and both 1994 ($F = 4.96$, $df = 13$, $P < 0.05$) and 1996 ($F = 10.39$, $df = 20$, $P < 0.005$). Analysis of variance detected no significant dif-

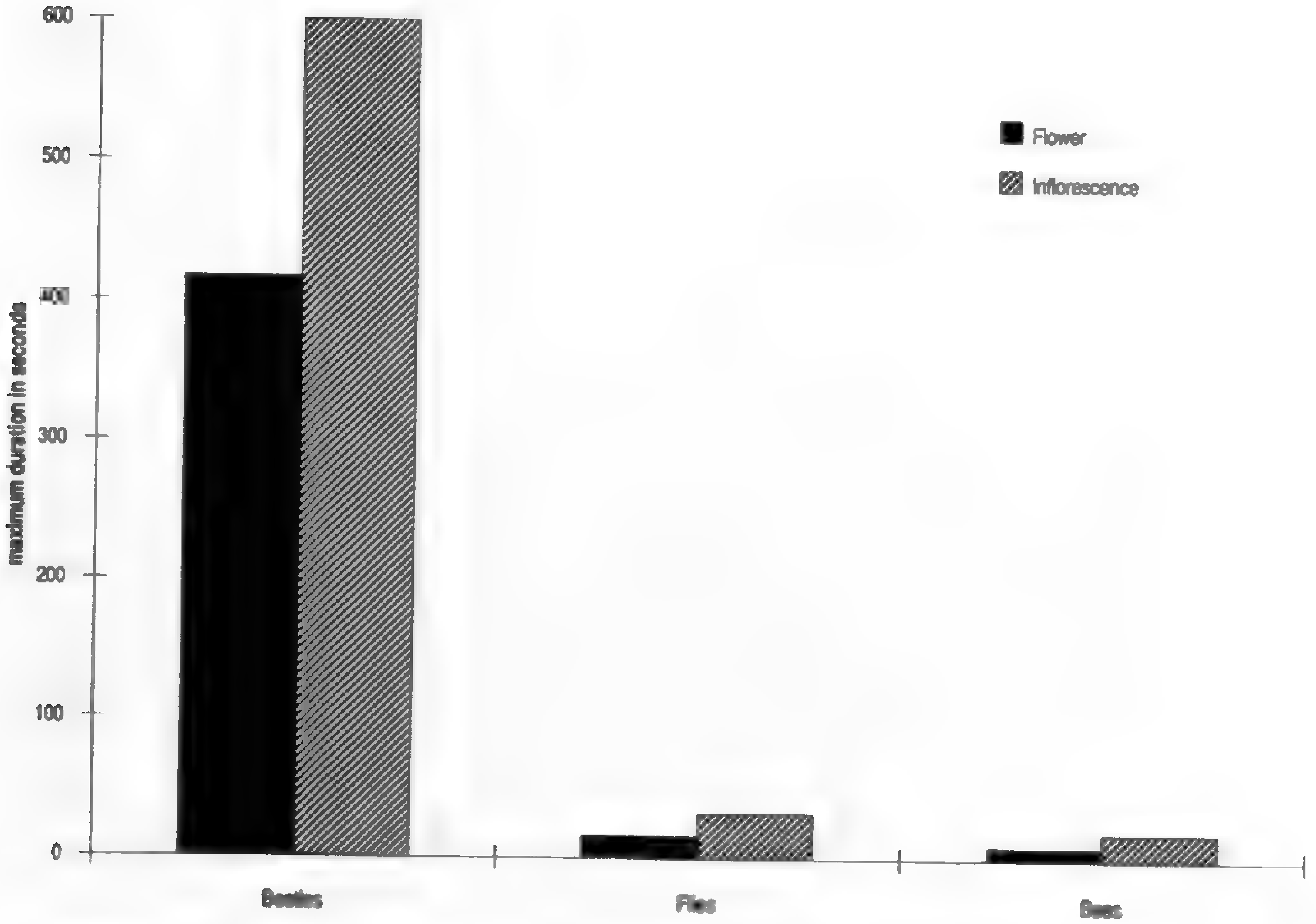

Figure 3. Comparison of the maximum observed duration of insect visits to flowers and inflorescences based on 27 ten-minute observation intervals (1994).

ference in fruit set between 1994 and 1996 (F = 0.037, df = 16, P = 0.849). A two-level nested Model II ANOVA performed on arcsine transformed fruit set data among individuals from three 1996 populations showed neither significant variance among populations nor an added variance component due to individuals. No correlations were found between fruit set within a population and either the size of the population or the overall plant density of the population (r = 0.024, n = 9; r = 0.016, n = 9, respectively). Nor was a significant correlation found between male plant densities and mean fruit set across populations (r = 0.139, n = 9).

Hand pollination experiments showed higher fruit set for 1996 ($\bar{x}$ = 80%, n = 28; Table 5) than for 1995 (64%, n = 8; Table 5). Analysis of variance on arcsine transformed data showed that fruit set variance for the 1996 hand pollinations was not significantly different from the controls (F = 1.913, df = 19, P = 0.18). However, significant differences were detected in fruit set variance between the intrapopulation and interpopulation crosses for 1996 (F = 5.892, df = 13, $P < 0.05$).

Berries averaged 9 mm in diameter when mature. Fruit ranged in weight from 0.07 to 0.68 g averaging 0.36 g. The mean seed

Table 5. Fruit set data and number of infructescences sampled for five 1995 and nine 1996 interpopulation crosses, five 1996 intrapopulation crosses, and open pollinated controls. * Populations represented as in Table 3 with the addition of BO = Bolton Road, CS = Cedar Swamp Road, S = Silver Lane, BR = Brewster Road, NR = North River Road, SE = South Eagleville Road, K = Knowlton Hill Road, W = Wormwood Site.

	Hand Pollination						Open Pollination Controls			
	Interpopulation Crosses				Intrapopulation Crosses 1996					
	1995		1996				1995		1996	
Population*	Sample	% Fruit Set	Sample	% Fruit Set	Sample	% Fruit Set	Sample	% Fruit Set	Sample	% Fruit Set
BO			3	97					4	67
CS	2	11			5	68	9	43	12	70
S			3	66					14	92
BR					1	45			7	85
NR			2	100	3	52			8	72
B	1	82	4	66			4	35	13	58
SE			3	51			2	87	1	74
A			1	78	2	80	5	39	4	55
K	1	100	7	74	4	25	11	56	17	100
W	3	52	2	95			8	57	3	80
C			3	99			3	40	4	53
DN	1	76					5	37		
Mean		64.2 ± 34.3		80.7 ± 17.8		54 ± 21.2		51 ± 18.0		73.3 ± 15.1

number per fruit was three (156 fruits from 6 sites in 1994). Seed weight ranged from 19 to 77 mg, averaging 32 mg (818 fruits from 6 sites in 1994). Seed weight typically accounted for about 25% of the fruit weight.

DISCUSSION

In *Smilax herbacea,* synchrony in pollen availability and stigma receptivity is critical to effective pollination and, therefore, to the success of dioecy as a reproductive strategy in this species. How is this accomplished in *S. herbacea*? Reproductive plants represent 60% of a population in a given season. Nearly 65% of these are male. Male plants typically inaugurate the reproductive season by one to several days, as in some other species (e.g., *Lindera benzoin*; Carloni 1982). In plants of both sexes, flower and inflorescence maturation on a single plant is staggered. In flowers of male inflorescences, pollen is dispensed in an incremental, timed-release pattern (i.e., all flowers do not open simultaneously), and, thus, pollen availability is extended over several days. Among inflorescences, pollen likewise becomes available gradually. The flowers of the basal inflorescences mature first, followed by incremental pollen release distally up the stem axis, resulting in overlap of pollen availability among inflorescences. Consequently, pollen of a single plant is available for up to several weeks. Because there is heterogeneity among males in inflorescence size and number as well as in temporal flowering patterns, pollen availability also overlaps within and among populations. Stigma receptivity in an individual flower lasts approximately three or four days and, as in males, there is incremental flower and inflorescence maturation. Therefore, we see that, with regard to flower production, the reproductive life spans of staminate and pistillate inflorescences are similar. However, because female plants typically have fewer inflorescences than male plants, the reproductive life span of a female plant will necessarily be shorter than that of a male plant. The more or less continual overlap of pollen production among male plants thus allows cooccurrence of pollen availability with stigma receptivity.

The overlapping of stigma receptivity by pollen production in plants of *Smilax herbacea* also can be considered in the context of the differential energetic costs of pollen production vs. the combined costs of ovule, seed, and fruit production. Greater reproductive costs are associated with female plants than with male plants of dioecious species (e.g., Cipollini and Whigham 1994; Nicotra 1996). This phenomenon may be reflected in the number of inflorescences and flowers produced by individuals of each sex and by cost in relation to plant size. It might be expected that more vigorous plants, either because they are more fit or because more resources are available to them, should be capable of producing more inflorescences and flowers. The significant correlation between both inflorescence and flower number with plant size among male plants seems to confirm this. However, this correlation is lacking among female plants indicating that, for females, the number of inflorescences and flowers is independent of the size of the plant. Larger female plants do not produce more reproductive structures than smaller plants. This constraint is likely due to greater reproductive costs in females, not in the cost of flowers, but in the cost of seeds and fruit that must develop and mature during the most stressful months of the season. Because male plants are both more prevalent and produce more flowers per plant than female plants, pollen to ovule ratios will likely be high within a site. Thus, the need for precise synchronization of reproductive effort between male and female plants is allayed by the presence of a greater proportion of male plants enhanced by the larger number of inflorescences, a feature facilitated by an apparent lack of constraint on flower production in males. Extended periods of overlap in flowering between the sexes may also be achieved via female plants that may overcome the constraint on flower production. This is evident in the occasional prolongation of flowering and, thus, of stigma receptivity in some female plants. Relatively more robust female plants infrequently produce an additional series of fewer-flowered inflorescences distal to the initial series and separated from it by several nodes. Observations of fruit set indicate that these additional inflorescences do not occur as a response to insufficient pollination of the first series of inflorescences. Their production may simply be dependent on the energetics of the plant (Grime 1977; Chapin 1980). This continued production could be developmentally preprogrammed, but contingent upon resource availability. The delayed flowering of this second series could either facilitate pollination by later flowering pollen donors or insure, in cases in which the female plants flower early in the absence of pollen donors, that at least some of the inflorescences are effectively pollinated.

When three assumptions are fulfilled, i.e., genetic determination of sex, lack of inbreeding, and lack of clonal growth, Fisher (1930) predicted a 1:1 zygotic sex ratio. The apparent absence of gender diphasy in *Smilax herbacea* implies probable heritable, genetic determination of sex rather than environmentally induced sex-switching (see Bawa and Beach 1981; Schlessman 1987). Further, the discovery of two hermaphrodite plants in 1995 (and their subsequent persistence) argues against sex determination by whole (X and Y) chromosomes as suggested by Mangaly (1968). As selfing, and therefore inbreeding, and clonal growth are also absent in the dioecious *S. herbacea,* Fisher's assumptions are fulfilled. Thus, we might suggest that the 2.3♂:1♀ sex ratio detected in this species arises post-zygotically in mature populations. With this assumption fulfilled, there are several possible explanations for the occurrence of the observed sex ratios. One likely explanation for male bias is the differential mortality of female plants. This possibility is supported by the conspicuous loss of seemingly robust females from among several populations between years. Our detection of a significant interaction between site and gender densities implies that site specific factors may also exert an influence on sex ratios. In dioecious species, environmental factors have been shown to influence male and female plants differently due to differences between the sexes in reproductive resource demands (Freeman et al. 1976; Lloyd and Bawa 1984; Niesenbaum 1992). The protraction of female reproductive life via fruit and seed production creates greater demands for resources in female plants than in males, and these demands occur during what are likely to be the more stressful summer months. Increased resource demand by females in concert with site-specific resource availability may explain increased female mortality, and this mortality may be responsible, in part, for variation in gender densities among sites.

Another possible explanation for the large male bias found for *Smilax herbacea,* viz., a difference in the flowering frequencies of males and females, is suggested by Allen and Antos (1993) who detected a significant male bias in their study of the dioecious Indian plum. In instances when females flower intermittently (i.e., do not always flower annually) or flower for the first time later in life than males, the presence of nonflowering females among all nonflowering plants can be suspected if a strong association exists between an increase in nonflowering individuals and an increase in gender bias across populations (also see Lloyd and Webb 1977). In *S. herbacea,* we report a significant positive slope in the regression line when proportions of flowering male plants are plotted against proportions of nonflowering plants in all populations examined in both years ($r = 0.7701$, $df = 15$, $P < 0.001$). This suggests that females may flower less frequently than males. However, neither intermittent flowering nor first flowering of female plants was observed during the course of this study.

Although pollen limitation in flowering plants is thought to be a major factor affecting fruit and seed set (Burd 1994), this does not appear to be the case in *Smilax herbacea.* Despite the relatively low frequency of insect visitation to female flowers, resource, rather than pollen, limitation is indicated primarily by the fact that fruit set was not improved by hand pollination. The same level of fruit set in populations with proportionately fewer males vs. those with proportionately more males argues further against pollen limitation. One might posit that pollination opportunities will be greater in sites where male plant densities are higher, and that fruit set might be positively affected by these differences. However, the lack of a correlation between male plant densities and fruit set argues against this. Even if these opportunities are indeed present, plants appear unable to take advantage of them.

Mellitophily, saprocantharophily, and sapromyophily were borne out in observations of this species. Highly mobile bees, in addition to flies, are likely to be the major pollinators of *Smilax herbacea.* Halictid and andrenid bees collect pollen for brood rearing and may exhibit a host-parasite relationship with the odor of carrion-flower (Faegri and van der Pijl 1979). This odor is detectable at some distance, and is thus the likely primary attractant for most pollinators leading them to the pollen reward. First flowering males are likely to recruit a guild of pollinators that will encounter a pollen reward (as in dioecious *Lindera benzoin*; Carloni 1982). It is then likely that the pollen reward for these recruits comes to be associated with the carrion odor present in both sexes. This association thereby promotes effective pollination via the deceptive strategies of the female plants. The presence of many flowers in simultaneous anthesis in inflorescences of both male and female plants creates high levels of attractant odor that is released into the environment by the tepals. Once in the vicinity of the flowers, visitors are adverted to conspicuous displays of pollen and, by deception in the case of females, to the greenish-white stigmas that appear to mimic pollen-laden anthers. This deception is fortified by the nearly identical appearance of the male and female inflorescences. In addition, the combination of easy accessibility, light to dull color, absence of nectar guides, strong odor, and presence in large inflorescences fits flowers characterized as those pollinated by small bees, flies, and beetles (Faegri and van der Pijl 1979).

Beetles are known to feed on pollen, and all beetle species observed in this study did so. Once a flower has opened, beetles often chew unopened anthers to get at the pollen reward, very likely shortening the reproductive life of the inflorescence. As noted above, the pollen is eaten rapidly by beetles, and this is one reason for males having pollen available for only a single day. The consumption of pollen was often so severe that inflorescences required bagging to ensure the availability of pollen for hand pollination experiments. The hard, relatively hairless bodies of beetles, and the fact that they seldom move among flowers or among plants, make them poor pollinators. In addition, the loss of pollen to beetle herbivory may be a greater cost than the benefit gained by beetle pollination.

The surviving hand pollination experiments resulted in a great deal of variation in fruit set. Unfortunately, many of the plants used in hand pollination experiments were destroyed by summer mowing. These included all 1995 intrapopulational attempts and, consequently, this resulted in low sample sizes. Significantly lower fruit set in 1995 was expected anyway due to widespread fungal infections promoted by the unusually wet conditions. The significant difference between intrapopulation and interpopulation crosses in the 1996 fruit set data (Table 4) might be a manifestation of inbreeding depression (Holsinger 1991, 1992). Fruit of *Smilax herbacea* is dispersed by songbirds (Martin et al. 1951). The large seeds probably are dropped principally within the site from which they were taken without passing through the bird's digestive system. Thus, the probability that genetically similar offspring will be dispersed within the same population may be higher than for long distance dispersal. Similarly, crosses between closely related individuals within populations may result in lower fruit set. Not surprisingly, fruit set was zero in all plants from which bags were not removed; thus, there is no evidence for apomixis (with the exception of agamospermy, the possibility of which is not addressed herein).

In summary, we have detected sex ratios in dioecious *Smilax herbacea* populations that are strongly male biased. Although sex expression probably is determined genetically, sex ratios most likely are influenced by female mortality, which in turn may be influenced by site characteristics. Male plants, in addition to being more prevalent than female plants, produce more flowers in more inflorescences than female plants. Male plants show continual inflorescence production throughout the breeding season and exhibit greater variation in the number of inflorescences produced per plant than female plants. Female plants, on the other hand, are restricted in the number of inflorescences they are able to produce, presumably due to the costs of fruit and seed production. Although abundant pollen is available, continuous and severe pollen predation by beetles restricts pollen availability in some flowers in all populations. The fact that hand pollination failed to improve fruit set implies that female plants are resource rather than pollen limited.

With respect to its pollination syndrome, *Smilax herbacea* can be characterized as a generalist. Pollen movement in *S. herbacea* begins with the attraction of insect pollen vectors via the carrion-like odor of both staminate and pistillate flowers. Pollinators then are adverted to the conspicuous inflorescences of both male and female plants, where they are drawn to the pollen reward in male flowers and deceived by the anther-mimicking stigmas in the female flowers. Results of this study implicate halictid and andrenid bees and anthomyiid and stratiomyiid flies as major pollinators and species in three families of beetles as potential minor pollinators.

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INVASION AND SPREAD OF *CALLITRICHE STAGNALIS* (CALLITRICHACEAE) IN NORTH AMERICA

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ABSTRACT. *Callitriche stagnalis* (Callitrichaceae) is a widespread aquatic species in the Old World, but an adventive component of the North American flora. Herbarium records are used to document the historical and current distribution of *C. stagnalis* in North America. It is hypothesized that the species initially established in North American seaports. The earliest collections of *C. stagnalis* in North America are from coastal regions in New York (1861), Oregon (1871), and New Jersey (1885). Prior to 1925, it is known from only a single noncoastal location (Montana, 1898). The rate of spread of *C. stagnalis* on the east versus west coast of North America differs. The species was well established on the east coast by the 1920s in New Jersey, New York, and southeastern Pennsylvania. On the west coast, only two locations (Oregon, British Columbia) were known by this time. The current distribution indicates that the species has spread about the same distance in both east and west coastal regions (400–500 miles): west coast, from the first documented locality in Clatsop Co., Oregon, to Napa Co., California, and east coast from Mercer Co., New Jersey, to regions of the St. Lawrence River in Quebec. Inland populations (Alabama, Montana, Wisconsin) are anomalous. Seed production is prolific in *C. stagnalis* and seeds are likely the principal unit of dispersal.

Key Words: *Callitriche stagnalis,* aquatic plants, nonindigenous species

Many species in the aquatic and wetland flora of North America are nonindigenous, having invaded from other regions (e.g., Les and Stuckey 1985; Stuckey 1966, 1970, 1974, 1979, 1980, 1981, 1985, 1993; Stuckey and Phillips 1970). These species new to an area or region are immigrants or invasive species that are often referred to as foreign, alien, or exotic members of the flora (Stuckey and Barkley 1993). Foreign plants can have drastic impacts on the ecology of aquatic and wetland environments, as exemplified by *Lythrum salicaria* L. (Lythraceae, cf. Stuckey 1980) and *Myriophyllum spicatum* L. (Haloragaceae, cf. Pieterse and Murphy 1993). However, most alien plant species have remained rather inconspicuous. Examples of the latter include *Lycopus europaeus* L. (European water-horehound; Stuckey and Phillips 1970) and *Veronica beccabunga* L. (European brooklime; Les and Stuckey 1985). Though not troublesome from a human perspective, it remains unknown what impact these exotic species may have on wetland plant communities and the ecology of wetland environments.

Callitriche stagnalis Scop. (water starwort) is a widespread aquatic plant of Europe, northern Africa (Clapham et al. 1987; Schotsman 1954, 1961a, b, 1967, 1972; Schotsman and Andreas 1980), Asia, Australia, New Caledonia, and New Zealand (Mason 1959). The species occurs in diverse aquatic and subaquatic habitats, e.g., marshes, stream and pool margins, and low, wet areas. Schotsman (1954, 1961a, b, 1972, 1985) has published works on various aspects of the taxonomy, biology, and distribution of the species in Europe.

The distribution of *Callitriche stagnalis* has evidently expanded considerably via human activities, and this species now seems to be the most widespread in the genus. Since the early part of this century it has been recognized that *C. stagnalis* is an adventive component of the North American flora. *Callitriche stagnalis* is readily distinguished from other amphibious species of *Callitriche* in North America (e.g., *C. heterophylla* Engelm. ex Hegelm. and *C. verna* L. emend. Kütz.) by its nearly round fruits in outline and the broad marginal wing that extends from the apex to around the base of each mericarp.

Fernald (1932), Rousseau (1968), and Svenson (1932) published brief accounts of the regional distribution of the species in eastern North America. Fassett (1951), in his revision of *Callitriche* in the New World, provided information on the distribution of the species in North America. Numerous specimens, however, that document a much wider distribution were evidently overlooked by Fassett. In addition, the species has spread considerably since the time of Fassett's paper.

The purpose of this paper is to use herbarium specimens to document the spread of *Callitriche stagnalis* in North America. Three questions are addressed: 1) When and where was *C. stagnalis* first documented in North America? 2) How has the distribution of the species expanded subsequently? 3) What is the current distribution of the species?

MATERIALS AND METHODS

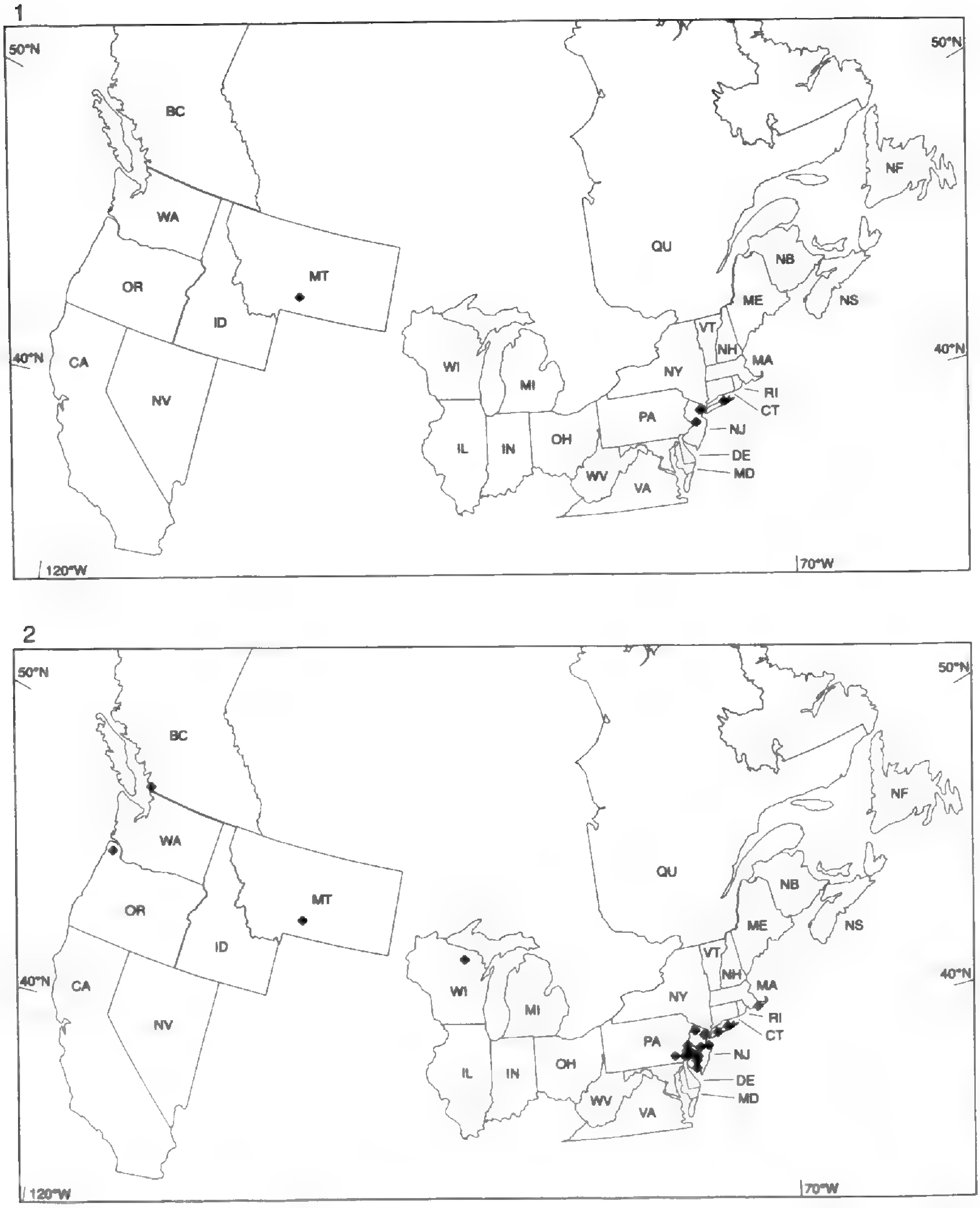
This study is based on examination of specimens from the following herbaria: ALA, ALTA, ARIZ, CAS, CLEMS, COLO, CONN, CU, F, FLAS, GH, IND, JEPS, KANU, KNK, LL, MAINE, MICH, MIN, MO, MT, NCU, NEBC, NHA, NY, OS, PH, RM, ROMO, RSA/POM, TEX, TRT, UBC, UNA, US, USFS, WCSU, WIS, WTU. It is difficult to confidently identify specimens of *Callitriche stagnalis* that lack fruit. Only specimens that have fruits are included in this study. Representative specimens that document the distribution are illustrated in Figures 1–4 and listed in Appendix 1.

The maps illustrate the distribution of *Callitriche stagnalis* for four periods: prior to 1900 (Figure 1), prior to 1926 (Figure 2), prior to 1951 (Figure 3), and current (Figure 4). These periods were selected to illustrate the progressive expansion of the species. The distribution maps are based exclusively on specimens examined, not on the published literature, although the latter is discussed in the text when relevant.

RESULTS

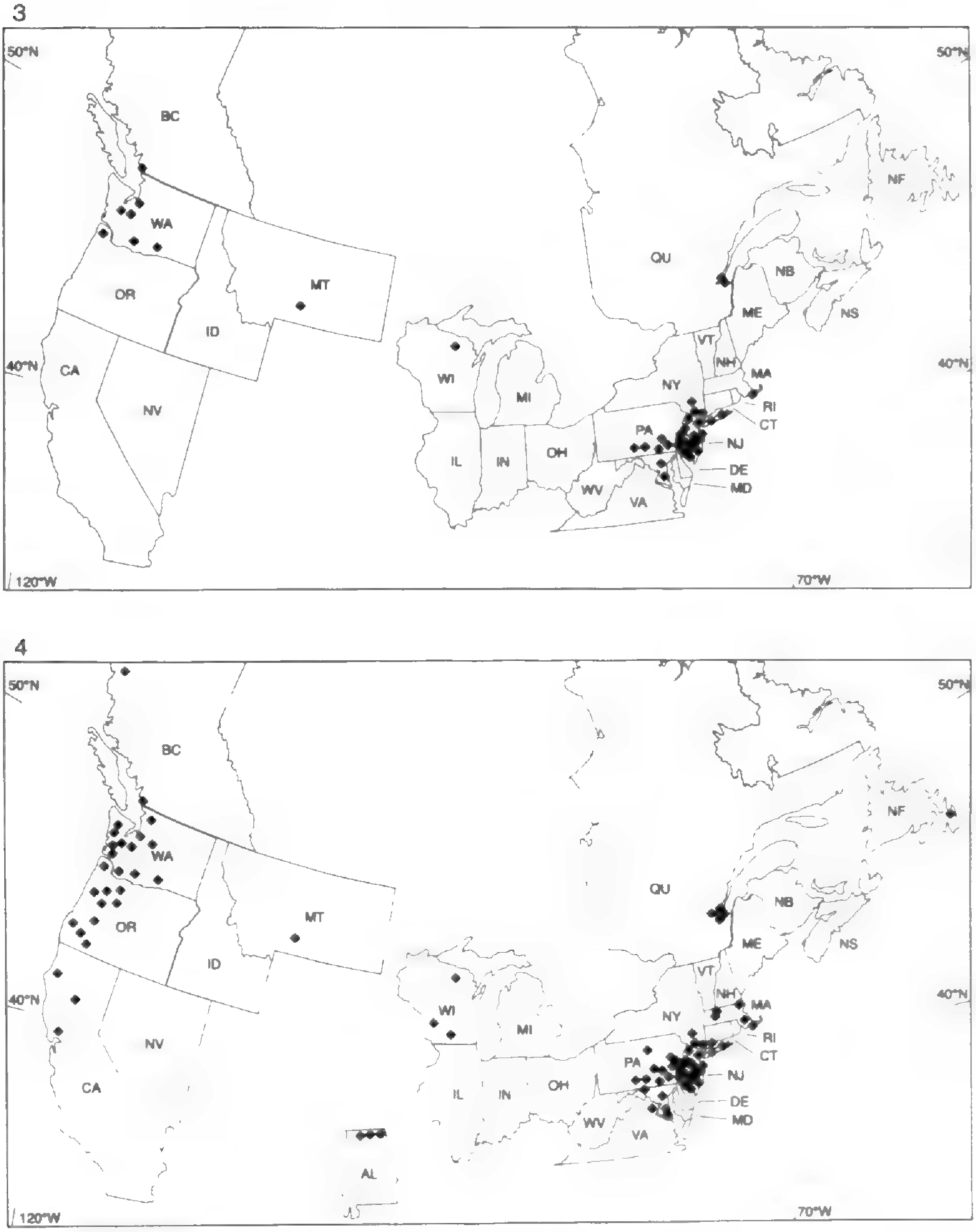
The earliest collection of *Callitriche stagnalis* in North America (1861) is from the state of New York (Figure 1; Appendix 1) although the locality from which it was collected is not known. An early collection without locality also exists from Oregon (1871). Interestingly, an early (1898) noncoastal location from Montana is also documented. Herbarium records further document that prior to 1900 the species occurred in New Jersey (Mercer Co., 1885; Bergen Co., 1891; Figure 1; Appendix 1). The first collection that can be attributed to a specific locality is from Suffolk Co., New York (Long Island, 1898; Appendix 1).

By 1925, the species is documented from 12 additional counties in eastern North America (Figure 2; Appendix 1): in New Jersey (Passaic Co., 1901; Camden Co., 1905; Gloucester Co., 1910; Cumberland Co., 1923; and Monmouth Co., 1923), New



Figures 1–2. Distribution of *Callitriche stagnalis* in North America (see Appendix 1). Selected regions of the United States and adjacent Canada are shown. Each diamond represents the first documentation for a county (U.S.) or region. Collections from New York (1861) and Oregon (1871) are not shown (see text). U.S. states and Canadian provinces are identified by postal abbreviations. 1. Collections prior to 1900. 2. Collections prior to 1926.

York (Nassau Co., 1926), and Massachusetts (Barnstable Co., 1911), in addition to five counties in Pennsylvania (Delaware Co., 1911; Montgomery Co., 1922; Philadelphia Co., 1923; Bucks Co., 1923; Chester Co., 1924). By 1925, the species is also doc-



Figures 3–4. Distribution of *Callitriche stagnalis* in North America (see Appendix 1). Selected regions of the United States and adjacent Canada are shown. Each diamond represents the first documentation for a county (U.S.) or region. 3. Collections prior to 1951. 4. Collections to present. Alabama is included in this figure but not in Figures 1–3.

umented from locations on the west coast of North America (Oregon, Clatsop Co., 1902, and British Columbia, New Westminster, 1916) and from an inland location in Wisconsin (Oneida Co., 1925), in addition to Montana.

Herbarium specimens indicate that by 1950 the distribution of *Callitriche stagnalis* had expanded considerably in the northeastern United States to include populations in four additional counties in New York and Pennsylvania and seven additional counties in New Jersey (Figure 3). In addition, two records in Maryland document the species for the first time in that state (Montgomery Co., 1942; Prince George's Co., 1943) and soon after (1952) in Virginia. Between 1926 and 1950 the species is also documented from four localities along the St. Lawrence Seaway in Quebec. Similarly, by 1950 specimens document the spread of the species in the northwestern United States (Washington: Benton Co., 1926; King Co., 1933; Pierce Co., 1934; Thurston Co., 1942; Yakima Co., 1942) and British Columbia (the region of Vancouver).

By the 1970s, the species had spread into the northernmost location from where it is currently documented on the east coast in Newfoundland (1968) and in states where it had previously been documented (Figure 4; Appendix 1). The northernmost location for the species on the west coast is from the Skeena River, British Columbia (Figure 4). Particularly notable are the records for the species occurring in three additional counties in Massachusetts, five in Pennsylvania, three in Washington, and two in Wisconsin. During this period it is documented from the southern United States (Alabama: Limestone, Madison, and Jackson Counties) as well as in California (Figure 4; Appendix 1).

The current distribution of *Callitriche stagnalis* (Figure 4) spans from Maryland to Massachusetts (one locality in Newfoundland, Canada) on the eastern seaboard, and more than 100 miles inland, especially in Pennsylvania. On the west coast the species is especially common in western parts of Oregon and Washington and in some areas of southwestern mainland British Columbia and Vancouver Island. In California it occurs in northern portions of the Central Valley and in the northern coastal region.

DISCUSSION

We interpret the data from herbarium specimen documentation as indicating that *Callitriche stagnalis* is not native to North America. Herbarium specimens document a progressive expansion of *C. stagnalis,* primarily in east and west coastal regions of North America, subsequent to invasion of the species circa the

1850s. The pattern observed for *C. stagnalis* is similar to that reported for numerous other wetland plant species (Stuckey 1993, and references therein).

Several authors reported on the early distribution of *Callitriche stagnalis* in North America. Svenson (1932) noted that *C. stagnalis* was a component of the northeast flora since at least 1905, citing specimens from Massachusetts, New York, New Jersey, and Pennsylvania. Fernald (1932) reported the species "while collecting on the always interesting tidal flats of the lower St. Lawrence" in Quebec. Fassett's (1951) account of the distribution of *C. stagnalis* was more thorough, although he evidently was not aware of specimens that documented an even broader distribution. Muenscher (1944) included Michigan on his map of the species, although no specimens have been documented in that state. Voss (1985) does not list this species in his flora of Michigan. Warrington (1980) reported the species from three areas in British Columbia: Vancouver, the region of Shuswap Lake (5 locations), and three locations on Vancouver Island. Specimens that may document the species on Vancouver Island were not seen by the authors. Fassett (1951) suggested that the early (1871) collection from Oregon might indicate that the species is native to that region. Although Cook (1985) listed the species as "questionably introduced" in North America, we contend that the data presented here confirm its non-native status.

Stuckey (1993) included *Callitriche stagnalis* in a general pattern of nonindigenous aquatics from Europe that occur primarily in the northeastern United States and eastern Canada, as well as the northwestern United States and adjacent Canada. Examples of other species that show similar patterns include *Lythrum salicaria,* which has become a troublesome invasive species, in addition to the less conspicuous *Butomus umbellatus* L., *Epilobium hirsutum* L., and *Veronica beccabunga.*

From the data presented herein it is evident that *Callitriche stagnalis* has undergone range expansion since first invading coastal regions. The species apparently arrived early in northern New Jersey, New York, and Oregon. Considerable regional expansion is evidenced in the mid-Atlantic states and Pacific Northwest. Currently, *C. stagnalis* exhibits its widest distribution in coastal regions in North America.

Knowledge of the invasions, subsequent spread, and establishment of alien species is valuable when making predictions of future distributions and possible ecological impact on native species. Several possible scenarios can explain the invasion and spread of *Callitriche stagnalis* in North America. Because this species is documented primarily from coastal regions during the first 60 years of its occurrence, a probable location of invasion is at seaport cities, where it may have arrived via ship ballast. Invasions of foreign species into coastal regions and subsequent migration inland have been reported for other aquatic and wetland species, among them *Lythrum salicaria* (Lythraceae; Stuckey 1980), *Rorippa sylvestris* (L.) Besser (Brassicaceae; Stuckey 1966), *Lycopus europaeus* (Lamiaceae; Stuckey and Phillips 1970), and *Veronica beccabunga* (Scrophulariaceae; Les and Stuckey 1985).

The number of times *Callitriche stagnalis* entered North America is not clear. Because invasions are a result of stochastic, largely unpredictable events, single and multiple introduction scenarios are equally probable. The species was present in both the northeast (New Jersey, New York) and northwest (Oregon) by the 1880s. It is possible that the species invaded twice, once on each coast. A single invasion into New York and subsequent spread (perhaps via shipping between east and west coasts) is also possible. Studies of the nature of the shipping industry during this time and the types of commerce taking place between these regions could provide a means of substantiating possible scenarios. Spread to new regions from earlier established populations or additional invasions could be invoked to account for subsequent population establishment along the St. Lawrence River in Quebec and perhaps in northern New York. The use of genetic markers (e.g., isozymes; cf. Soltis and Soltis 1989) could provide insight on the number of invasions as well as patterns of subsequent spread.

With the majority of the current distribution in coastal regions, the inland populations (Alabama, Montana, Wisconsin) of *Callitriche stagnalis* are anomalous. It is not possible to assess whether the relatively early (1925) introduction of the species into Wisconsin is a consequence of spread from coastal areas or represents an additional invasion. In northern Alabama the three county locations are along the Tennessee River. These locations may represent spread of the species from other North American locations. No direct link by shipping or other commerce is apparent between this region and Europe that would explain the fairly recent (1980) documentation. R. Haynes (pers. comm.) suggests that the species may be native to several natural springs in northern Alabama. The early (1898) documentation from Montana could be used to support an argument for the species being native to North America. Interestingly, only a single collection from 1898 documented the presence of *C. stagnalis* in Montana [a specimen (23 Aug 1979, *Lackschewitz 9219,* RM) from Ravalli Co., Montana, lacks fruit but may be *C. stagnalis*]. Although the inland populations are difficult to explain, we feel that the pattern of spread of the species in North America over the last century, documented by herbarium specimens, indicates that it is not native to North America.

The rate of spread of *Callitriche stagnalis* on the east versus west coast seems to differ. Herbarium specimens indicate that the species became well established on the east coast by the 1920s in New Jersey, Long Island (New York), and southeastern Pennsylvania. In contrast, on the west coast, only two locations (Oregon, British Columbia) are documented by this time. Even so, the species has spread about the same distance in both eastern and western coastal regions: west coast, from the first documented locality in Clatsop Co., Oregon, to Napa Co., California, and east coast from Mercer Co., New Jersey, to regions of the St. Lawrence River in Quebec.

Reproductive systems play a central role in the spread of exotic species (e.g., Baker and Stebbins 1965, and references therein). The reproductive biology of *Callitriche stagnalis,* especially in its foreign range, is poorly understood. For example, whether the species grows as an annual or perennial form is dependent upon climate. Martinsson (1991) reported an annual habit for plants grown under greenhouse conditions in Sweden. By inference, the same is also possible for natural populations in that cold climate region. In contrast, the species seems to be perennial in the northeastern United States. One of the authors (Philbrick) has observed green plants along streams in southwestern Connecticut in January. Similarly, Svenson (1932) reported plants as "green and thriving" in midwinter on Long Island (New York), and Fernald (1950) also reported the species as perennial.

The growth form of this amphibious species indicates that it can spread readily within a local area via clonal growth. Plants in shallow water, or on moist soil, exhibit extensive horizontal growth, producing numerous nodal roots and developing a dense mat of intertwining stems. However, unlike many clonal species of aquatic and wetland plants (Philbrick and Les 1996; Sculthorpe 1967), species of *Callitriche* do not produce specialized vegetative propagules. Dispersal of plant fragments is possible, although their involvement in the geographic spread of the species is not known.

Seed production is prolific in *Callitriche stagnalis* in both its native and adventive (North American) ranges. Seeds seem to be the principal units of dispersal and geographic spread. Philbrick (1989) and Philbrick and Anderson (1992) have shown that the flowering period of *C. stagnalis* in North America ranges from April to November, and seed production is near 100% as geitonogamous pollination (pollination between flowers at a node) predominates. Thus, seed can be produced after a single plant becomes established. Possible means of seed dispersal are not known. Reports exist that seeds of species of *Callitriche* are eaten by ducks (cf. Fassett 1957), although it is not clear what role ducks, or birds in general, play in dispersal (birds' feet?). Human activities may actively transport seeds of *C. stagnalis.* This species often occurs in roadside ditches in Oregon and Washington. Seeds may well be transported in wet mud by vehicle traffic in these regions.

Species of *Callitriche* are not known to be troublesome aquatic weeds. In their book on aquatic weeds, Pieterse and Murphy (1993) consider only one species (*C. verna* in Japan) as being occasionally troublesome. Current observations suggest that *C. stagnalis* will become a nuisance in some regions of North America. Hitchcock and Cronquist (1973) listed the species as being occasional in Oregon, but did not list it as occurring in Washington. Yet, the species is now widespread in the western portions of both states. In Oregon, it seems to be even more widespread than herbarium records indicate (R. Halse, pers. comm.). *Callitriche stagnalis* is now also common in the lower Fraser River Valley in British Columbia (A. Ceska, pers. comm.) and in the region around the city of Quebec (L. Brouillet, pers. comm.). Because the species regularly produces dense clonal stands in irrigation canals and roadside ditches, it will predictably have an impact on native aquatic plant species.

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APPENDIX 1: SPECIMENS OF *CALLITRICHE STAGNALIS* IN CANADA AND THE UNITED STATES THAT DOCUMENT ITS DISTRIBUTION IN A STATE, COUNTY, OR REGION WITHIN A PROVINCE.

Specimens are organized alphabetically by country, and state or province. Only the first documented collection from each county or region within a province is listed. Specimens noted with * have incomplete or unclear label information and are not included in Figures 1–4.

Canada. BRITISH COLUMBIA: New Westminster, 10 Jun 1916, *Henry 9068* (GH); Skeena R., 13 Sep 1974, *Pojar s.n.* (UBC); NEWFOUNDLAND: St. John's Co., 17 Jun 1968, *Scott 219* (UBC); QUEBEC: Bellechasse Co., Bellechasse, 26 Aug 1931, *Victoria & Germai 45062* (CU); Desjardins Co., Lauzon, 1 Aug 1950, *Desmarais 1077* (MT); Quebec metropolitan area, Point Pizeau, 8 Aug 1950, *Desmarais 1881* (MT); l'Ile d'Orleans Co., St. Pierre, 25 Jul 1936, *LeGallo 422* (MT).

United States. ALABAMA: Jackson Co., 6 Jun 1980, *Meigs 782* (UNA); Limestone Co., 20 May 1980, *Meigs 547* (UNA); Madison Co., 28 May 1980, *Meigs 661* (UNA); CALIFORNIA: Butte Co., 19 May 1988, *Oswald 3323* (CONN, WCSU); Humboldt Co., 9 Jun 1987, *Philbrick 2044* (CONN, WCSU); Napa Co., 29 Aug 1968, *Ackley s.n.* (CAS); CONNECTICUT: Fairfield Co., 20 Sep 1994, *Philbrick 4613* (CONN, WCSU); MARYLAND: Montgomery Co., 16 May 1942, *Killip 36567* (MO); Prince George's Co., 10 Jun 1943, *Hermann 10827* (NY); St. Mary's Co., 30 Sep 1984, *Philbrick 1386* (CONN, WCSU); Washington Co., 13 Jun 1981, *Hill 10318* (NY); MASSACHUSETTS: Barnstable Co., 2 Aug 1911, *Pennell 3381* (GH); Essex Co., 11 Jul 1957, *Harris 12997* (NEBC); Franklin Co., 25 May 1965, *Eaton & Eaton 5711* (NEBC); Hampshire Co., 7 Jun 1960, *Livingston s.n.* (NCU); Plymouth Co., 22 May 1980, *Sorrie 351* (NEBC); MONTANA: Stillwater Co., 18 Sep 1898, *Blankinship s.n.* (WTU); NEW JERSEY: Atlantic Co., 22 Feb 1937, *Long 49629* (PH); Bergen Co., 11 Jul 1891, *Nash s.n.* (NY); Camden Co., 20 Aug 1905, *Stone 7382* (PH); Cumberland Co., 12 Aug 1923, *Long & Bassett s.n.* (PH); Gloucester Co., 16 May 1910, *Long 3396* (PH); Hunterdon Co., 27 Jun 1972, *Roberts 2433* (PH); Mercer Co., 20 Jan 1885, *Peters s.n.* (PH); Middlesex Co., 17 Jun 1945, *Koster D16-23-3* (PH); Monmouth Co., 2 Sep 1923, *Beals & Bassett 7665* (CAS); Passaic Co., 31 May 1901, *Svenson 4478* (MU); Salem Co., 5 Jun 1932, *Long 37637* (OS); Somerset Co., 4 Jun 1945, *Chrysler s.n.* (PH); Union Co., 29 Jun 1936, *Kezer s.n.* (NY); Warren Co., 12 Aug 1949, *Shaeffer 31450* (PH); NEW YORK: * "Thusk"(?), Jul 1861, *J.G.B. 383* (F); Nassau Co., 15 Jun 1926, *Ferguson 2173* (NY); Orange Co., 27 Aug 1936, *Muenscher & Curtis 5746* (CU); Putnam Co., 23

Aug 1936, *Muenscher & Curtis 5745* (CU); Suffolk Co., 4–5 Jul 1898, *Clute 111* (NY); Ulster Co., 17 Jun 1926, *Ferguson 4879* (NY); OREGON: * 1871, *Hall 460* (F); Benton Co., 18 May 1980, *Halse 2162* (ARIZ); Clackamas Co., 13 Jun 1987, *Philbrick 2067* (CONN, WCSU); Clatsop Co., 20 Aug 1902, *Sheldon S.11215* (F); Coos Co., 11 Jun 1987, *Philbrick 2057* (CONN, WCSU); Douglas Co., 11 Jun 1987, *Philbrick 2059* (CONN, WCSU); Jackson Co., 11 Jun 1987, *Philbrick 2053* (CONN, WCSU); Lane Co., 12 Jun 1987, *Philbrick 2061* (CONN, WCSU); Lincoln Co., 15 Nov 1952, *Steward 6228* (CAS); Linn Co., 12 Jun 1987, *Philbrick 2063* (CONN, WCSU); Polk Co., 13 Jun 1987, *Philbrick 2066* (CONN, WCSU); PENNSYLVANIA: Bedford Co., 2 Sep 1939, *Berkheimer 1445* (PH); Berks Co., 19 Apr 1941, *Wilkins 6555* (PH); Bucks Co., 28 Aug 1923, *Long 29099* (PH); Carbon Co., 8 Jul 1951, *Wherry s.n.* (PH); Chester Co., 5 Jul 1924, *Long 31290* (PH); Cumberland Co., 30 May 1929, *Ward s.n.* (PH); Dauphin Co., 24 Jun 1952, *Berkheimer 13497* (PH); Delaware Co., 13 May 1911, *Eckeldt s.n.* (PH); Lancaster Co., 19 Jul 1948, *Fassett 27852* (PH); Lehigh Co., 8 Jul 1960, *Shaeffer 61135* (PH); Lycoming Co., 21 Jun 1955, *Wahl 15909* (PH); Montgomery Co., 15 Oct 1922, *Long 26781* (PH); Northampton Co., 28 Jul 1960, *Shaeffer 61498* (PH); Philadelphia Co., 17 May 1923, *Meredith s.n.* (PH); VIRGINIA: Fairfax Co., 25 May 1952, *Fosberg 34488* (RSA); WASHINGTON: Benton Co., Aug 1926, *Jones 369* (WIS); Cowlitz Co., 15 Jun 1987, *Philbrick 2071* (CONN, WCSU); Gray's Harbor Co., 6 Sep 1957, *Thorne 19122* (WTU); Jefferson Co., 20 Jun 1987, *Philbrick, Philbrick & Busse 2090* (CONN, WCSU); King Co., 28 Jul 1933, *Thompson 9612* (WTU); Kittitas Co., Sep 1965, *Spellenberg 1313* (F); Pacific Co., 15 Jun 1987, *Philbrick 2077* (CONN, WCSU); Pierce Co., 29 Apr 1934, *Jones 4620* (WTU); Thurston Co., 12 Jun 1942, *Meyer 2161* (MO); Wahkiakum Co., 15 Jun 1987, *Philbrick 2075* (CONN, WCSU); Whatcom Co., 15 Jul 1965, *Sutherland 1083* (WTU); Yakima Co., 15 Oct 1942, *Hoover 5998* (US); WISCONSIN: Dane Co., 13 Aug 1958, *Hartley 5322* (WIS); Monroe Co., 19 Aug 1956, *Hartley 2487* (WIS); Oneida Co., 25 Aug 1925, *Davis s.n.* (WIS).

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ANTENNARIA ALPINA (ASTERACEAE: INULEAE): REVISION OF A MISUNDERSTOOD ARCTIC-ALPINE POLYPLOID SPECIES COMPLEX

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ABSTRACT. Canonical discriminant analysis was used to determine: (1) whether *Antennaria alpina* occurs in North America or not; (2) which character or combination of characters could best be used to distinguish members of the *A. alpina* and *A. media* polyploid complexes; and (3) whether infraspecific taxa warrant formal recognition in *A. alpina.* The results of this investigation indicate that *A. alpina* does occur in North America. The main morphological distinctions between the two aforementioned polyploid complexes are the presence of scarious tips at the ends of middle to distal peduncular leaves in *A. alpina,* these being absent in *A. media,* and the shape of the involucral bracts. The analyses support the recognition of infraspecific taxa in *A. alpina.* To maintain consistency with other recent revisions of polyploid complexes in the genus, the rank of subspecies (*A. alpina* subsp. *alpina,* subsp. *canescens,* and subsp. *porsildii*) was selected. In addition to minor quantitative differences, the three subspecies differ with respect to the degree, distribution, and type of pubescence on the basal leaves.

Key Words: *Antennaria alpina* subsp. *alpina, A. alpina* subsp. *canescens, A. alpina* subsp. *porsildii,* Asteraceae, Inuleae, polyploid species complex, canonical discriminant analysis

Over the past fifteen years five of the *Antennaria* (L.) Gaertner polyploid species complexes which occur, in whole or in part, in arctic or arctic-alpine North America have been revised. These include *A. neodioica* E. L. Greene (Bayer 1989a; Bayer and Stebbins 1982), *A. rosea* E. L. Greene (Bayer 1989b; Chmielewski and Chinnappa 1988a), *A. monocephala* DC. (Chmielewski and Chinnappa 1991), *A. frieseana* (Trautv.) Ekman (Bayer 1993; Chmielewski 1994a), and *A. media* E. L. Greene (Chmielewski 1997). Only two major North American arctic-alpine polyploid species complexes remain in need of revision, that of *A. alpina* (L.) Gaertner and *A. pulcherrima* (Hook.) E. L. Greene. The former complex, which is the focus of this investigation, has had no less than a dozen infraspecific taxa described in North America alone (Cronquist 1955; Fernald 1924; Rydberg 1917; Scoggan 1979; Welsh 1974). Despite the recognition of these taxa, as well as the occurrence of *A. alpina s.l.* in Scandinavia and Greenland, some past authorities (Greene 1898; Malte 1934; Porsild 1965) questioned whether this purported circumpolar complex (Ekman 1927) occurred in North America. Disagreement among authors was, and still is in part, attributable to the green-black phyllaries shared by members of both the *A. alpina* and *A. media* polyploid complexes, as well as the fact that members of each complex exhibit a high degree of morphological variability and thus morphological overlap. This variability is due, in part, to polyploidization (Bayer 1984, 1990a; Bayer and Stebbins 1981, 1987; Chinnappa 1986; Chmielewski and Chinnappa 1988b, c, 1990), as well as the extensive geographic ranges over which the complexes extend (Bayer and Stebbins 1987; Chmielewski 1997). Because considerable morphological overlap was believed to exist between the two complexes, Jepson (1925) proposed the recognition of *A. media* as a variety of *A. alpina.* Bayer (1993) and others before him (Fernald 1924; Greene 1898; Rydberg 1900) noted that two characters distinguished *A. alpina* from *A. media.* First, and most importantly, is the presence of flat, scarious tips (flags) at the ends of the middle to distal peduncular leaves (historically referred to as cauline leaves) in the former species, these being mostly absent in the latter. Second, the phyllaries of pistillate *A. alpina* are typically acute, whereas in *A. media* they are blunt. Both complexes were treated as distinct by Bayer and Stebbins (1993) in their synopsis of North American representatives of the genus. In addition, *A. alpina* was recognized by Bayer and Stebbins (1993) as being composed of innumerable apomictic clones; thus they recommended that circumscription should follow a broad species concept, noting that further studies were necessary prior to finalizing treatments for the two complexes.

The objectives of this investigation were to determine: (1) whether *Antennaria alpina* occurs in North America; (2) which, if any, character or combination of characters could best be used to distinguish between members of the *A. alpina* and *A. media* complexes; and (3) whether any infraspecific taxa warrant formal recognition in *A. alpina.*

MATERIALS AND METHODS

Herbarium specimens of *Antennaria alpina s.l.* from Scandinavia and Greenland, presumed *A. alpina* from North America, and *A. media s.l.* from North America (as defined and utilized in Chmielewski 1997) used in the phenetic study were borrowed from C, CAN, CAS, CM, DAO, DAV, GH, IDS, MONTU, MT, NDG, RENO, RM, S, SD, SLRO, UAC, UBC, US, UT, and WS (Holmgren et al. 1990). Representative specimens of the *A. media* polyploid species complex were cited previously (Chmielewski 1997); representative specimens and types of *A. alpina s.l.* are listed in the Taxonomic Treatment. The taxa and their names adopted at the conclusion of the investigation [*A. alpina* subsp. *alpina, A. alpina* subsp. *canescens* (Lange) Chmielewski, and *A. alpina* subsp. *porsildii* (E. Ekman) Chmielewski] will be used throughout the body of the text for the sake of clarity, except when used in reference to previous publications. Specimen selection and identification follow the methodology of Chmielewski (1993). No *a priori* restrictions were placed on the total number of specimens deemed necessary to represent the range of variation within *A. alpina s.l.* Qualitative characters used to identify specimens to species prior to analysis included: habit (presence or absence of stoloniferous growth); the presence or absence of flat, scarious tips (flags) at the ends of the middle to distal peduncular leaves; degree, distribution, and type of pubescence on basal leaves; glandularity, if any; color, shape, and texture of the phyllaries; exsertion of the style; and occurrence of papillae on the cypsela (historically referred to as an achene).

Data were collected for 16 quantitative characters. These included the vegetative characters basal leaf length and basal leaf width; the vegetative-reproductive characters peduncle length, number of peduncular leaves, peduncular leaf length, peduncular leaf width, number of capitula, involucre length, outer phyllary length, outer phyllary width, inner phyllary length, and inner phyllary width; and the reproductive characters cypsela length, pappus length, style length, and corolla length. The selection of these characters was based on their usefulness in previous revisions of the genus by this laboratory (Chmielewski 1993, 1994b, 1995a, b, 1996, 1997; Chmielewski and Chinnappa 1988a, 1991; Chmielewski et al. 1990a, b). Only pistillate plants were utilized in the phenetic analysis because inclusion of the few available staminate collections, specifically from *Antennaria media s.l.*, necessitated the exclusion of style length, which was deemed unacceptable. Each data matrix was, therefore, complete for all characters (see Bayer 1992 and Chmielewski and Chinnappa 1992 for a discussion on the acceptability and use of incomplete data matrices in phenetic studies of *Antennaria*).

Prior to initiating the various statistical procedures, length measurements were transformed to their logarithms (base 10) and count data to their square roots (Cooley and Lohnes 1971; Gilbert 1968). Classificatory discriminant analysis, using the SAS (SAS Institute Inc. 1989) DISCRIM procedure, was first used to classify specimens identified *a priori* to their respective taxonomic group. Several options, including list, simple, pool, splool, crossvalidate, crosslist, and posterr were included with this procedure. Correct identification rates (Pimentel 1979; Pimentel and Frey 1978) were used as indicators of separation between or among groups of specimens. The classification criterion was used subsequently to assign additional specimens to one of the previously defined groups. This *a posteriori* assignment of specimens assumes that they do indeed belong to one of the *a priori* groups of specimens and not to a taxonomic group excluded from the study.

Canonical discriminant analysis was used to summarize among-group variation. Bivariate plots of canonical variate scores were used to facilitate visualization of discontinuities between and among groups of specimens (DeltaPoint Inc. 1992). Descriptive statistics reported in the taxonomic treatment were calculated using the SAS UNIVARIATE procedure (SAS Institute Inc. 1989).

Three data matrices were analyzed during the course of the investigation. The first matrix consisted of 371 specimens and initially was used to test whether North American specimens believed to be part of the *Antennaria alpina* polyploid complex (n = 142) could be distinguished from North American *A. media s.l.* (n = 229). Results based on the analysis of these data would: (1) demonstrate whether the two taxa are morphologically distinct (based on quantitative versus qualitative differences); and (2) define quantitative characters that could best be used to differentiate between members of the two complexes.

The second data matrix consisted of the same 142 specimens of North American *Antennaria alpina* used in the first data matrix and specimens of *A. alpina* from either Greenland (n = 69) or Scandinavia (n = 39). Results based on the analysis of these data would: (1) demonstrate whether geographic separation correlates with selection for different morphotypes; (2) define quantitative characters that could best be used to differentiate among individuals from each of the three geographic areas; and (3) possibly provide information on the directionality of postglacial colonization of Greenland by members of the polyploid complex.

The third data matrix included the 250 specimens of data matrix two. These were divided into the following three groups: (1) 182 specimens previously treated as *Antennaria alpina* were treated as *A. alpina* subsp. *canescens*; (2) 18 specimens previously treated as Greenland *A. alpina* were treated as *A. alpina* subsp. *porsildii*; and (3) the remaining 50 specimens were treated as *A. alpina* subsp. *alpina,* regardless of their geographic origin. Type collections of *A. alpina* var. *cana* Fernald & Wiegand (n = 3), *A. alpina* var. *canescens* Lange (n = 1), *A. alpina* var. *glabrata* J. Vahl (n = 1), *A. arenicola* M. O. Malte (n = 1), *A. atriceps* Fernald (n = 2), *A. brevistyla* Fernald (n = 1), *A. canescens* f. *fastigiata* Böcher (n = 1), *A. columnaris* Fernald (n = 3), *A. confusa* Fernald (n = 8), *A. congesta* M. O. Malte (n = 1), *A. glabrata* (J. Vahl) Greene f. *ramosa* A. E. Porsild, *A. longii* Fernald (n = 6), *A. porsildii* E. Ekman (n = 4), *A. sornborgeri* Fernald (n = 1), *A. subcanescens* Ostenfeld ex M. O. Malte (n = 2), and *A. vexillifera* Fernald (n = 3) were used in the *a posteriori* component of the analysis. Specimens of *A. alpina* f. *latifolia* E. Ekman and *A. alpina* var. *ungavensis* Fernald were overmature (florets had detached from the receptacle) and, because of the missing data, could not be included as part of the *a posteriori* analysis. Results based on analysis of these data were expected to: (1) demonstrate whether the recognition of infraspecific taxa is warranted; (2) define those quantitative characters which could best be used to differentiate among the infraspecific taxa; and (3) facilitate assignment of the respective type collections of unassigned taxa to one of the recognized infraspecific taxa.

RESULTS

Two *a priori* complexes (North American *Antennaria alpina* s.l. and *A. media* s.l.). Evaluation of the discriminant function through the use of cross-validation identification indicated that 83.3% of the 371 specimens utilized were assigned with the highest Geisser assignment probability (mean ± standard deviation) to the correct *a priori* species complex (*Antennaria alpina s.l.,* 86.6%, 0.923 ± 0.110; and *A. media s.l.,* 81.2%, 0.918 ± 0.122).

Table 1. Summary of Mahalanobis distances between pairs of geographic groups and their associated squared distance F-values (in parentheses).

	Greenland	Scandinavia
North America	2.16 (5.88)	6.02 (10.81)
Greenland		5.23 (7.65)

The Mahalanobis distance between species complexes (3.18) and associated squared distance F-value (16.73) indicate that their respective centroids (−1.10 and 0.68) were significantly different ($P < 0.0001$). The canonical correlation of the first discriminant function (0.66), which squared is the proportion of the total variance explained by the function (0.43), indicates that the recognition of these two complexes explains a low amount of the overall variation. Except for peduncle length, characters with high loadings on the first canonical axis (style length, inner phyllary length, involucre length, and corolla length) were associated with either the capitulum or the floret.

Three *a priori* groups (*Antennaria alpina s.l.* from North America, Greenland, and Scandinavia). Evaluation of the discriminant function through the use of cross-validation identification indicated that 83.6% of the 250 specimens were assigned with the highest Geisser assignment probability (mean ± standard deviation) to the correct *a priori* geographic group (*Antennaria alpina s.l.* from: North America 78.2%, 0.930 ± 0.115; Greenland 87.0%, 0.909 ± 0.114; and Scandinavia 97.4%, 0.951 ± 0.107). The Mahalanobis distances between pairs of geographic groups (Table 1) and associated squared distance F-values indicated that all between-geographic group comparisons of centroids (Figure 1) were significantly different ($P < 0.0001$). The first canonical variate accounted for 67.3% of the among-group variation. The canonical correlation coefficients associated with the first two canonical axes (0.65 and 0.52) indicate that the overall goodness of fit between the variables and classification is weak. Characters that had high loadings on the first canonical axis (pappus length, style length, involucre length, inner phyllary length, and corolla length) are associated with either the floret or the capitulum and may best be used to separate the groups of specimens. Characters that had high loadings on the second canonical axis included number of capitula, basal leaf width, and outer phyllary width.

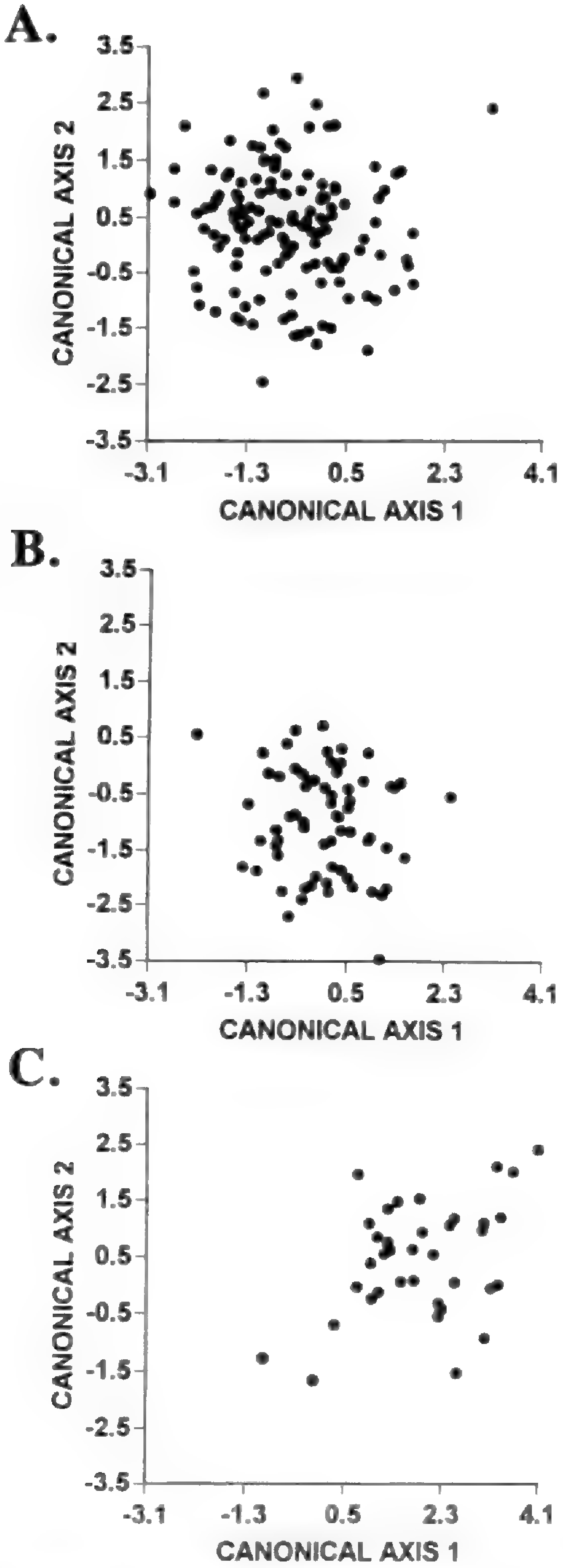

Figure 1. Ordination of canonical variate scores and summary of group centroids for *Antennaria alpina s.l.* from: (A) North America (−0.57, 0.34); (B) Greenland (0.10, −0.97); and (C) Scandinavia (1.88, 0.47).

Table 2. Summary of Mahalanobis distances between pairs of infraspecific taxa and their associated squared distance F-values (in parentheses).

	subsp. *canescens*	subsp. *porsildii*
subsp. *alpina*	4.01 (9.24)	12.57 (9.77)
subsp. *canescens*		6.43 (6.19)

Three *a priori* groups (*Antennaria alpina* subsp. *alpina*, subsp. *canescens*, and subsp. *porsildii*). Evaluation of the discriminant function through the use of cross-validation identification indicated that 89.6% of the 250 specimens were assigned with the highest Geisser assignment probability (mean ± standard deviation) to the correct *a priori* infraspecific taxon (*Antennaria alpina* subsp. *alpina*, 96.0%, 0.951 ± 0.098; subsp. *canescens*, 86.8%, 0.951 ± 0.103; and subsp. *porsildii*, 100%, 0.999 ± 0.000). The Mahalanobis distances between pairs of infraspecific taxa (Table 2) and associated squared distance F-values indicated that all between-infraspecific group comparisons of centroids (Figure 2) were significantly different ($P < 0.0001$). The first canonical variate accounted for 69.3% of the among-group variation. The canonical correlation coefficients associated with the first two canonical axes (0.66 and 0.50) indicate that the overall goodness of fit between the variables and classification is weak. Characters that had high loadings on the first canonical axis included number of peduncular leaves, peduncle length, basal leaf width, number of capitula, and peduncular leaf width. Three characters (number of peduncular leaves, peduncle length, and number of capitula) can best be used to separate subsp. *alpina* and subsp. *canescens* from subsp. *porsildii*. Basal leaf width is only somewhat useful in separating subsp. *alpina* from both subsp. *canescens* and subsp. *porsildii*. Eight characters (outer phyllary length, inner phyllary length, inner phyllary width, outer phyllary width, corolla length, cypsela length, pappus length, and involucre length) had high loading on the second canonical axis. These vegetative-reproductive characters associated with the capitulum and reproductive characters associated with the floret are selectively useful in separating the subspecies. Generally, subsp. *alpina* and subsp. *porsildii* are more similar to each other with respect to these characters than either is to subsp. *canescens*. Therefore, the former five and latter eight characters can best be

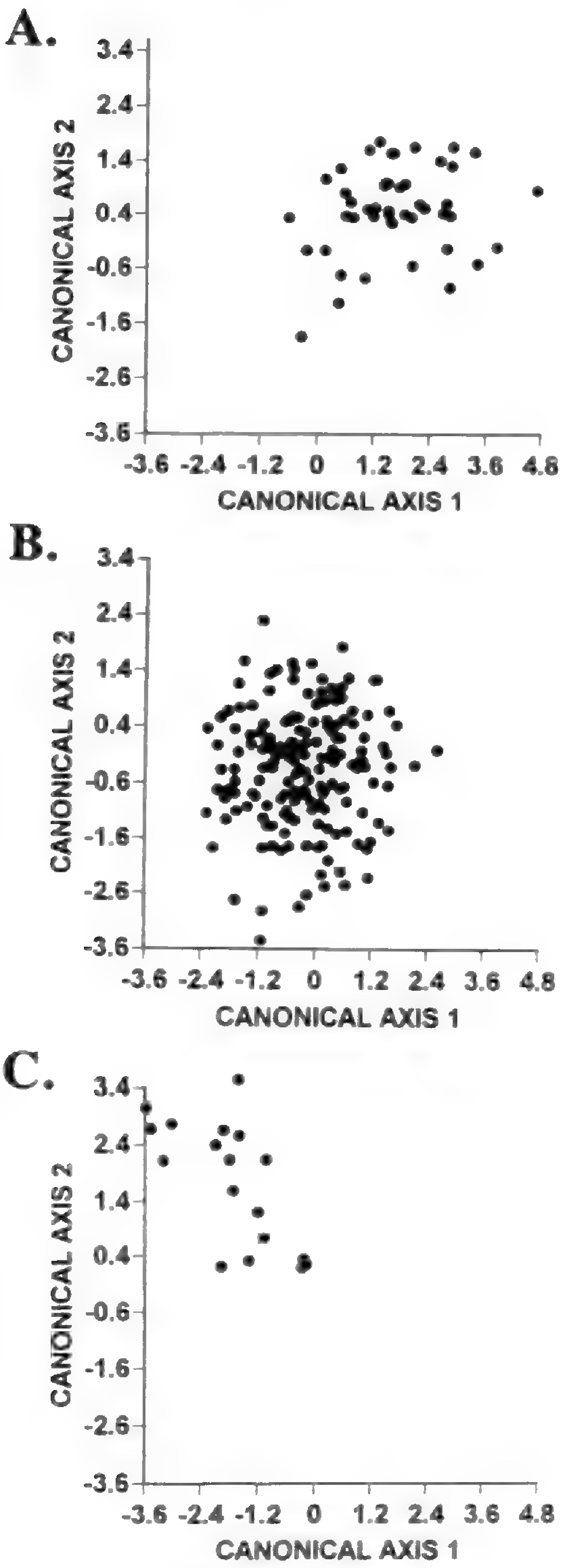

Figure 2. Ordination of canonical variate scores and summary of group centroids for *Antennaria alpina:* (A) subsp. *alpina* (1.57, 0.51); (B) subsp. *canescens* (−0.26, −0.31); and (C) subsp. *porsildii* (−1.76, 1.73).

Table 3. Summary of descriptive statistics (mean ± standard deviation) for *Antennaria alpina* subsp. *alpina* (n = 50), *A. alpina* subsp. *canescens* (n = 182), and *A. alpina* subsp. *porsildii* (n = 18).

	subsp. *alpina*	subsp. *canescens*	subsp. *porsildii*
Peduncle length (cm)	11.6 ± 2.9	7.9 ± 3.0	6.2 ± 1.9
Number of peduncular leaves	9.2 ± 1.9	7.4 ± 1.9	5.9 ± 1.5
Peduncular leaf length (mm)	14.6 ± 3.1	11.3 ± 2.5	11.7 ± 1.7
Peduncular leaf width (mm)	1.9 ± 0.5	1.5 ± 0.4	1.5 ± 0.3
Basal leaf length (mm)	13.3 ± 2.7	10.5 ± 3.1	12.8 ± 3.4
Basal leaf width (mm)	3.2 ± 0.7	2.7 ± 0.7	2.5 ± 0.5
Number of capitula	5.6 ± 1.7	4.4 ± 1.4	2.7 ± 1.4
Involucre length (mm)	6.3 ± 0.7	5.8 ± 0.5	6.2 ± 0.5
Outer phyllary length (mm)	4.4 ± 0.7	4.0 ± 0.6	4.6 ± 0.6
Outer phyllary width (mm)	1.1 ± 0.2	1.1 ± 0.2	1.2 ± 0.3
Inner phyllary length (mm)	5.7 ± 0.6	5.3 ± 0.5	5.9 ± 0.5
Inner phyllary width (mm)	0.7 ± 0.1	0.7 ± 0.2	0.8 ± 0.1
Cypsela length (mm)	1.2 ± 0.3	1.1 ± 0.3	1.1 ± 0.2
Pappus length (mm)	5.4 ± 0.5	4.9 ± 0.4	5.4 ± 0.4
Style length (mm)	5.0 ± 0.7	4.4 ± 0.5	4.7 ± 0.4
Corolla length (mm)	4.2 ± 0.5	3.8 ± 0.4	4.3 ± 0.5

used in various combinations to differentiate among the three subspecies of *A. alpina* (Table 3).

A posteriori assignments of type collections believed to be included within this polyploid complex are also summarized (Table 4).

The geographic distributions of specimens representing the three subspecies accepted at the conclusion of the study are illustrated in Figures 3–5.

DISCUSSION

Analysis of the first data matrix was intended to address the question of whether *Antennaria alpina* occurs in North America or not. Arguably, one of the major difficulties associated with answering this question is deciphering to which morphological entity previous authors were referring.

Greene (1898) was apparently the first North American author to formally note that *Antennaria alpina* was common in the mountains of Norway and Greenland, but that it was not known to occur on the North American continent. Nelson (1901) concurred. Fernald and Wiegand (1911) opined that further investigation would indicate that the species was circumpolar, and that many of the described arctic and alpine taxa would better be treated as geographic variants or infraspecific taxa of *A. alpina.* Holm (1920) noted that it would "seem very unnatural" for the circumpolar *A. alpina* not to occur on the North American continent, as it is frequent in Greenland. Fernald (1924) asserted that typical *A. alpina* (*A. alpina* var. *typica* Fernald) occurred in arctic America south to Kangalaksiorvik Bay, Labrador. Malte (1934) concluded that the Kangalaksiorvik Bay specimen cited by Fernald (1924) was *A. angustata.* Upon locating the type of *A. alpina* (described from Lapland as *Gnaphalium alpinum* L.) in LINN, Malte (1934) concluded that the species did not occur in North America, at least insofar as he had not seen a North American specimen which exactly matched the type collection. Bayer (1993) supported this viewpoint, but only if a strict typological species concept were adopted. He further judged that the *A. alpina* species complex was composed of innumerable apomictic clones, and recommended a broad species circumscription until a final decision on its treatment could be reached.

Resolution of the North American occurrence question has been confounded, in part, by the green-black phyllaries shared by members of the *Antennaria alpina* and *A. media* polyploid complexes, as well as the fact that each of the complexes is phenotypically plastic. Plasticity is due in part to a preponderance of agamospermous reproduction (Holm 1920) in each of the complexes.

Several characters have been used during the past century to differentiate between *Antennaria alpina* and *A. media.* Greene (1898) noted that involucral bracts in Old World *A. alpina* are decidedly narrower and more acuminate than they are in its western American homologue *A. media.* Rydberg (1900) concluded that *A. media* differs from *A. alpina* in that the spatulate leaves of the former are conspicuously tomentose on both sides, whereas they are adaxially glabrous in the latter. Fernald (1924) added to the character suite of North American *A. alpina,* stating that the upper cauline leaves terminate in an oblong, glabrous, scarious appendage. Thus, the two main distinctions between the species are the presence of scarious tips at the ends of middle to distal peduncular leaves in *A. alpina,* these being absent in *A. media,* and the shape of involucral bracts (acute in the former and blunt in the latter). Bayer and Stebbins (1993) supported the use of these characters in their North American synopsis of the genus.

Table 4. Summary of *a posteriori* assignments and probabilities for type collections of *Antennaria*. Type collections were ultimately assigned through the use of diagnostic qualitative characters as well as the results of this analysis.

Type Collection	Type Designation	Subspecies	Probability
A. alpina var. *cana*	Holotype (GH)	*canescens*	0.9999
	Isotype (CAN 106057)	*canescens*	0.5088
	Paratype (GH)	*canescens*	1.0000
A. alpina var. *canescens*	Lectotype (C)	*canescens*	0.6072
A. alpina var. *glabrata*	Lectotype (C)	*porsildii*	0.9997
A. arenicola	Holotype (CAN 105983)	*canescens*	0.8138
A. atriceps	Lectotype (CAN 105927)	*canescens*	0.8138
	Isolectotype (CAN 506917)	*canescens*	0.5710
A. brevistyla	Holotype (GH)	*canescens*	1.0000
A. canescens f. *fastigiata*	Holotype (C)	*canescens*	0.9993
A. columnaris	Holotype (GH)	*canescens*	1.0000
	Isotype (MT)	*canescens*	1.0000
	Paratype (MT)	*canescens*	1.0000
A. confusa	Holotype (GH)	*canescens*	0.9998
	Isotype (MT)	*canescens*	0.9998
	Paratype (MT)	*canescens*	1.0000
	Paratype (MT)	*canescens*	1.0000
	Paratype (MT)	*canescens*	1.0000
	Paratype (MT)	*canescens*	0.9986

Table 4. Continued.

Type Collection	Type Designation	Subspecies	Probability
	Paratype (MT)	*canescens*	1.0000
	Paratype (MT)	*canescens*	1.0000
A. congesta	Holotype (CAN 105922)	*canescens*	1.0000
A. glabrata f. *ramosa*	Lectotype (CAN 281573)	*canescens*	1.0000
A. longii	Holotype (GH)	*canescens*	0.9969
	Paratype (GH)	*canescens*	0.9999
	Paratype (GH)	*canescens*	0.9846
	Paratype (GH)	*canescens*	1.0000
	Paratype (GH)	*canescens*	1.0000
	Paratype (CAN 106059)	*canescens*	1.0000
A. porsildii	Holotype (C)	*porsildii*	0.9988
	Paratype (C)	*porsildii*	0.9994
	Paratype (C)	*porsildii*	0.9986
	Paratype (S)	*canescens*	1.0000
A. sornborgeri	Holotype (GH)	*canescens*	0.9973
A. subcanescens	Holotype (CAN 106127)	*canescens*	0.9764
	Isotype (GH)	*alpina*	0.9080
A. vexillifera	Holotype (GH)	*canescens*	0.9998
	Isotype (MT)	*canescens*	0.7078
	Isotype (CAN 106056)	*canescens*	1.0000

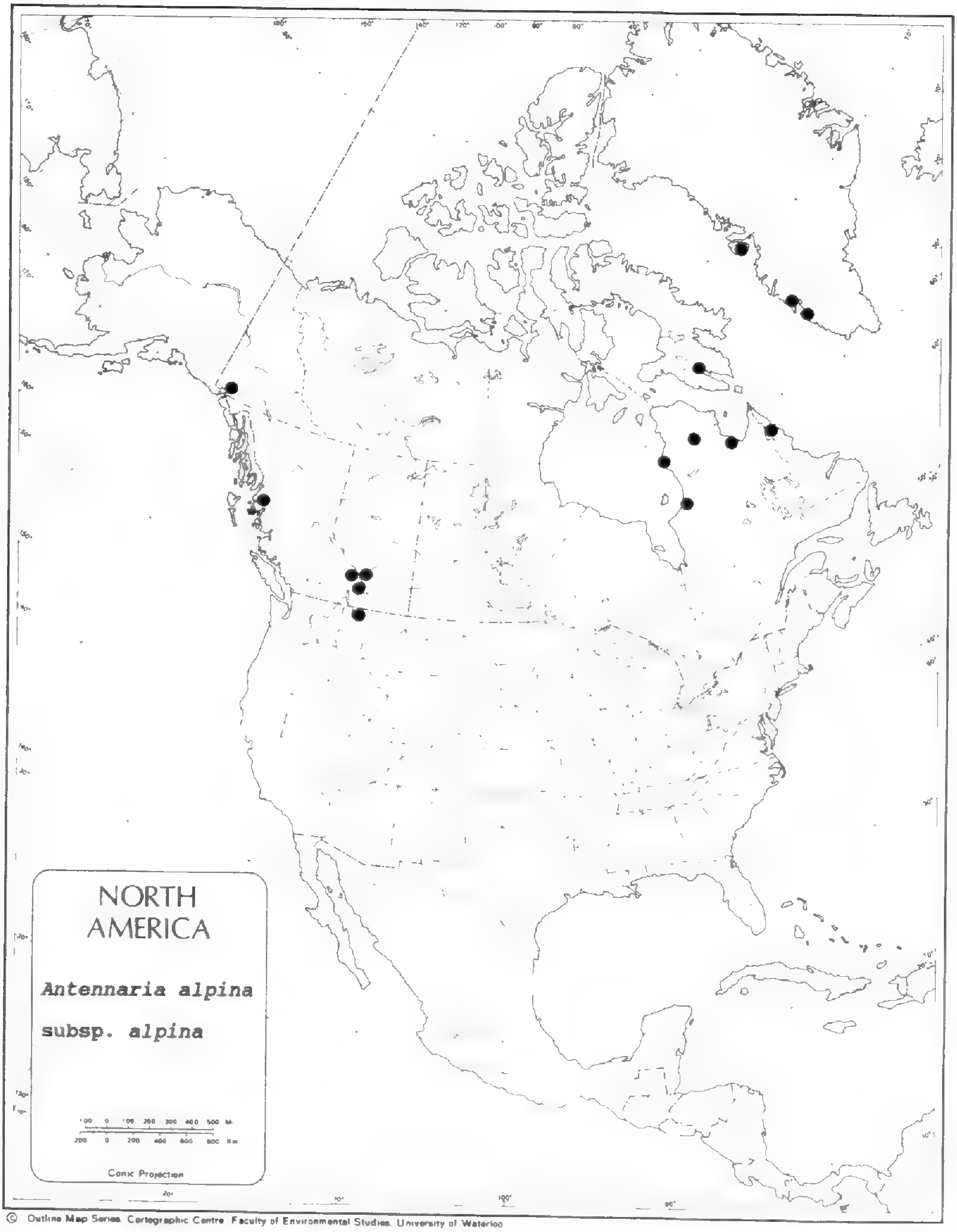

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Figure 3. North American distribution of *Antennaria alpina* subsp. *alpina*. The Scandinavian distribution of the subspecies approximates that illustrated by Hultén (1968) for *A. alpina* and is therefore not presented here. Bullets may represent more than one collection.

Having now completed re-evaluations of both the *Antennaria alpina* and *A. media* (Chmielewski 1997) complexes using quantitative morphological characters, it is evident that as circumscribed here both occur in North America and their distributions

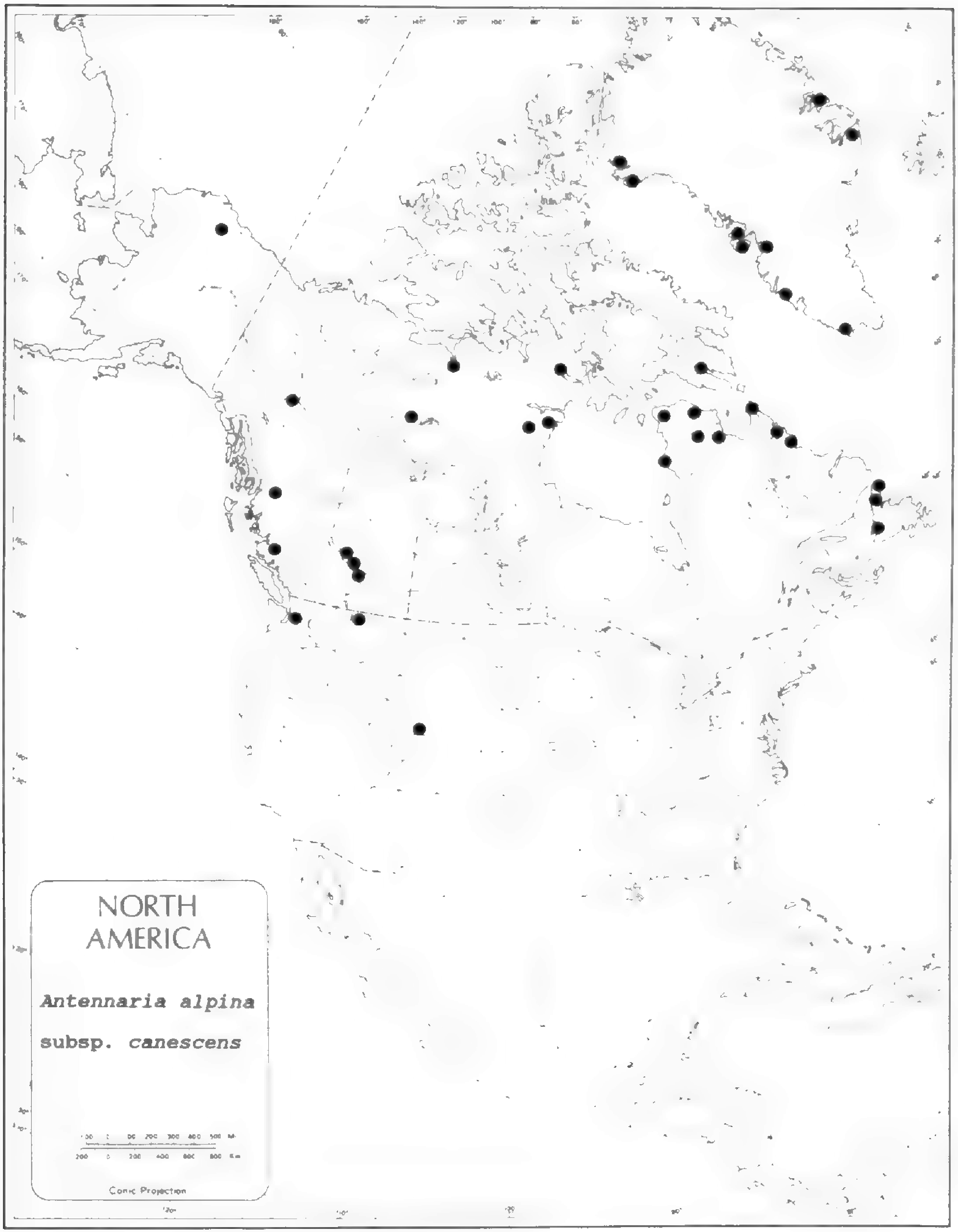

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Figure 4. North American distribution of *Antennaria alpina* subsp. *canescens*. The Scandinavian distribution of the subspecies approximates that illustrated by Hultén (1968) for *A. alpina* var. *canescens* and is therefore not presented here. Bullets may represent more than one collection.

overlap, at least partially. Further, in addition to the qualitative characters previously stated, the capitula of *A. alpina* are typically more lustrous and brighter (especially in the brown phyllaried form) than in *A. media*, and the capitulescence is typically more

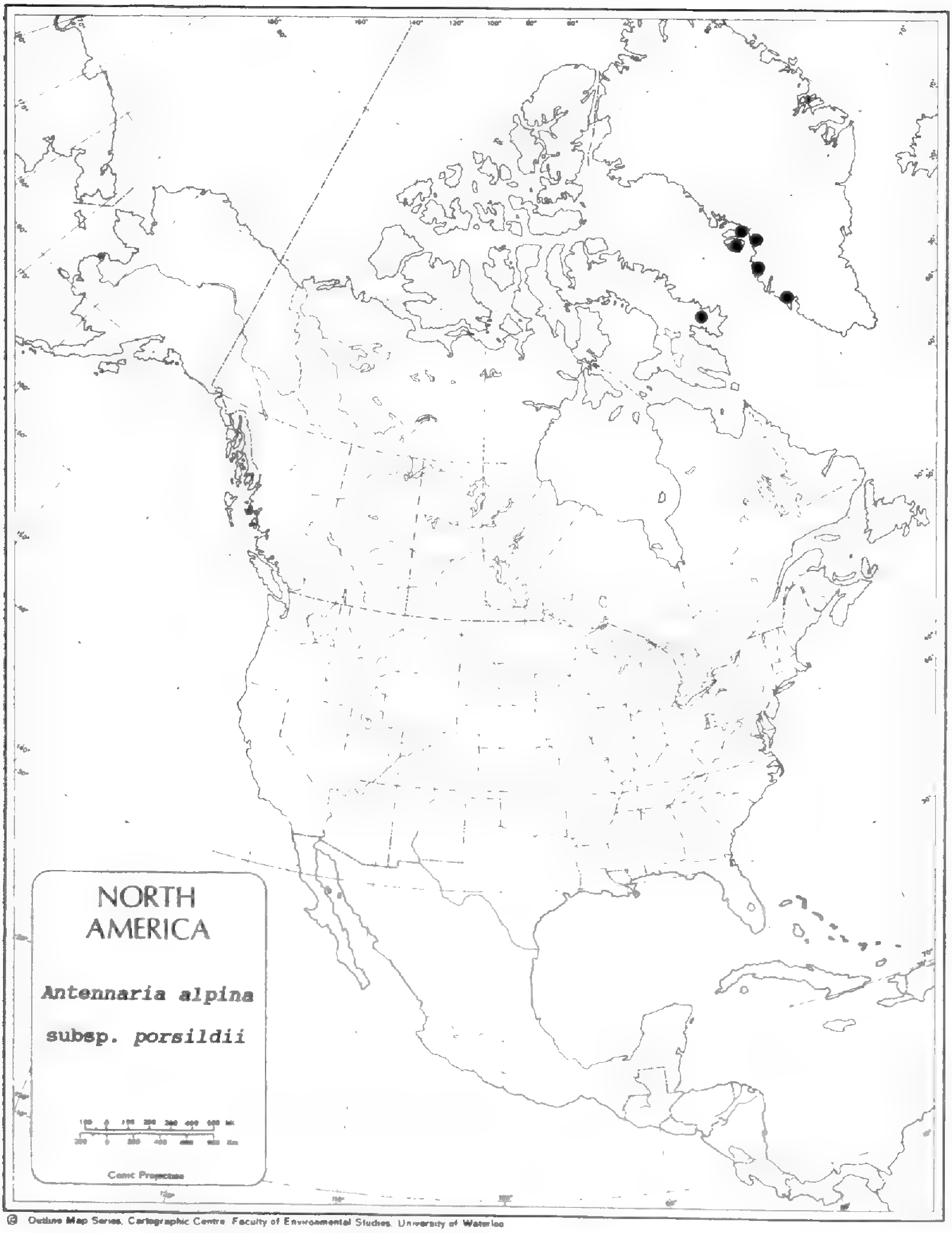

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Figure 5. North American distribution of *Antennaria alpina* subsp. *porsildii.* The Greenland distribution of the subspecies approximates that presented by Böcher (1963) for *A. glabrata.* Bullets may represent more than one collection.

open in the former than in the latter. The two complexes also differ in style length, inner phyllary length, involucre length, and corolla length. The low amount of total variance (43%) explained by the first discriminant function, because of the recognition of these two complexes, indicates that the selected quantitative characters are only somewhat useful in delimiting the complexes. Thus, the previously stated qualitative characters remain the best with which to separate members of the two complexes.

Holm (1920) noted that more or less well-marked varieties will sometimes result because of polymorphism attributable to the vast geographic distribution of species. Thus, the second data matrix was used first to assess whether patterns of geographic variation were discernible in *Antennaria alpina* and warranted infraspecific recognition, and second, to evaluate previous hypotheses relative to the colonization of Greenland by the genus.

Three characters (pappus length, style length, and involucre length) can best be used to separate Scandinavian specimens from either Greenland or North American specimens. The single misclassified (not assigned to the correct geographic group) Scandinavian specimen was assigned to the Greenland group. Distinguishing between the North American and Greenland specimens is a more difficult task, these specimens differing predominantly in basal leaf width, number of capitula, and outer phyllary width (those characters which had high loadings on the second canonical axis). Misclassified North American specimens were assigned twice as often to the Greenland than to the Scandinavian group, whereas misclassified Greenland specimens were approximately equally distributed between the geographic groups. The low amount of the total variance explained by the first discriminant function, because of the recognition of three geographic groups, indicates that the specimens should be divided on the basis of something other than geography.

R. T. Porsild (1914) regarded *Antennaria alpina* as an old species that found its way to Greenland after the glacial period, probably over Smith Sound, where the crossing may have taken place during an epoch with milder climate than now rules in Greenland. In reviewing the available literature Ekman (1927) regarded the floral immigration to Greenland to be pincer-like. That is, plants in eastern Greenland migrated from the east, presumably before the last glacial period, along an isthmus running from Scandinavia across Iceland to Greenland, whereas plants in western Greenland migrated from the northern regions of North America. A. E. Porsild (1965) opined that, in the Old World, not only was *A. alpina* endemic to the Scandinavian mountains, but that the disjunct or bicentric ranges of *A. glabrata* (J. Vahl) Greene, *A. porsildii,* and

A. ungavensis (Fernald) M. O. Malte suggested that they must have occupied at least part of their present-day range in pre-Pleistocene time. Bayer (1990b) proposed that *Antennaria* per se could have migrated to Eurasia any time from the Middle Miocene to the end of the Pleistocene. Further, he believed it more likely that the genus migrated to Eurasia via Beringia instead of across a European–North American land bridge. The occurrence of species such as *A. nordhagiana* Rune & Rönning in presumed glacial refugia in northern Norway suggested that they evolved prior to the Quaternary because they inhabited primarily unglaciated regions (Rune and Rönning 1956). Based on similarities between and among geographic groups, the results of the present study suggest that colonization of Greenland by *A. alpina* followed the pincer-like immigration proposed by Ekman (1927). It is, however, difficult to address the question of global distribution in *A. alpina* based on literature citations alone, as distribution is intimately tied to the manner in which the taxon was delimited by the respective author(s).

The third set of analyses dealt specifically with the delimitation of infraspecific taxa within *Antennaria alpina.* Although numerous infraspecific taxa were previously proposed for *A. alpina,* the results of this study support the recognition of only three. In keeping with the criteria utilized in recent revisions of the genus (e.g., Bayer 1990a; Bayer and Stebbins 1982; Chmielewski 1993, 1994a, b, 1995a, b, 1997; Chmielewski and Chinnappa 1988a, 1991) the following subspecies are recognized: *A. alpina* subsp. *alpina, A. alpina* subsp. *canescens* (Lange) Chmielewski, and *A. alpina* subsp. *porsildii* (E. Ekman) Chmielewski.

Both qualitative and quantitative characters may be used, in part, to distinguish among the three subspecies, but the former are unquestionably the better. Qualitative characters include: (1) the degree to which stoloniferous growth has developed and (2) whether the basal leaf surfaces are glabrous or not. Stolons are short and leafy in subsp. *porsildii,* are variable in subsp. *canescens,* but generally well developed, and are well developed in subsp. *alpina.* The basal leaves of subsp. *alpina* are bright green and glabrous or glabrate adaxially and villous or tomentose abaxially. The basal leaves of subsp. *canescens* are permanently villous-tomentose both adaxially and abaxially. In subsp. *porsildii* the entire plant, including both surfaces of the basal leaves, is glabrous.

Quantitative characters which can best be used to distinguish between and among the subspecies were summarized previously. Some of these characters, such as peduncle length, number of peduncular leaves, and number of capitula, are more sensitive to environmental cues than are the strictly reproductive characters of the florets. Plasticity in response to environmental factors, as well as polyploidization, undoubtedly reduces the usefulness of some of these characters for separation of the subspecies. Despite their differences, the quantitative characters do tend to exhibit greater uniformity between and among subspecies than occurs with the qualitative characters.

Analysis of the third data matrix also allowed for the *a posteriori* assignment of type collections of several taxa to one of the subspecies adopted here. Except for the assignment of *Antennaria brevistyla* and *A. glabrata* f. *tomentosa,* this treatment is in agreement with that proposed by Bayer and Stebbins (1993) for the listed taxa, insofar as they both support their inclusion in *A. alpina.* Bayer and Stebbins (1993) tentatively assigned *A. brevistyla* to *A. rosea* Greene subsp. *confinis* (Greene) R. Bayer, whereas I assign the species to subsp. *canescens. Antennaria glabrata* f. *tomentosa* E. Ekman (= *A. hudsonica* M. O. Malte) is included here as part of subsp. *canescens,* but was previously assigned to *A. monocephala* subsp. *angustata* (Greene) Hultén (Bayer and Stebbins 1993; Chmielewski and Chinnappa 1991). Disagreement between the present study and the synopsis for the genus presented by Bayer and Stebbins (1993) occurs predominantly among those species which were not included as part of this study (*A. bayardi* Fernald, *A. brunnescens* Fernald, *A. compacta* M. O. Malte, *A. foggii* Fernald, *A. pallida* E. Nelson, *A. pedunculata* A. E. Porsild, *A. rousseaui* A. E. Porsild, and *A. stolonifera* A. E. Porsild) because they were previously assigned to other taxa (see Chmielewski 1995a, b, 1997). Further, Bayer and Stebbins (1993) also included *A. intermedia* (Rosenv.) A. E. Porsild and *A. wiegandii* Fernald in synonymy with *A. alpina,* whereas it is my opinion that the former should be included within *A. pallida* (Chmielewski 1995a) and the latter within *A. howellii* Greene subsp. *gaspensis* (Fernald) Chmielewski (Chmielewski 1995b).

Antennaria alpina is essentially a gynoecious species. The staminate plant was previously reported as being exceedingly rare, having been found only a few times in France, Scandinavia, and

Alaska (Holm 1920) and more recently in the Canadian Yukon Territory (Bayer 1993). The occurrence of staminate specimens of *A. alpina* from France seems unlikely since the species does not appear to occur there (Bayer and Stebbins 1987; Hultén 1968). These species distributions suggest that the reports are for staminate *A. dioica* and not *A. alpina.* Because staminate specimens of *A. alpina* were reported to occur only in association with *A. dioica* in Scandinavia (Ekman 1927), it also seems reasonable to question whether they were simply misidentified as belonging to the former species when in reality they belonged to the latter. However, Nygren (1950) did conclude that in some areas of the Scandinavian mountains (in the Paldsa area) staminate plants are not rare. The Alaskan specimens to which Holm (1920) refers could reasonably be either *A. monocephala* subsp. *monocephala* or *A. frieseana* (Trautv.) Ekman subsp. *alaskana* (M. O. Malte) Hultén, as reference is made to each as being part of *A. alpina.* Finally, the staminate specimen cited as *A. alpina* by Bayer (1993) from the Yukon Territory was treated as *A. media* subsp. *media* by Chmielewski (1997). Staminate plants have not been reported from either northeastern Canada (Porsild 1965) or Greenland (Ekman 1927; Porsild 1965). Not having seen any staminate specimens of *A. alpina* among the thousands examined during the course of this investigation, I tend to believe that they do not exist.

Asexual reproduction in *Antennaria alpina* occurs either through the production of vegetative offsets or through agamospermy. Viable seeds apparently are produced in abundance (Holm 1920). This apomict may, however, give rise to staminate plants via chromosome segregation (Bayer and Stebbins 1987). The staminate plants could, in turn, then pollinate pistillate plants if the two come into contact. The lack of functional pollen (Porsild 1965) in presumed staminate specimens of *A. alpina* does, however, negate the possibility of fertilization.

Polyploid agamic complexes such as *Antennaria alpina* have evolved through hybridization events between and among sexual species. Several hypotheses have been put forth relative to the origin of the complex, including: (1) derivation from *A. dioica* (Rune and Rönning 1956); (2) hybridization among the diploids *A. aromatica* Evert, *A. densifolia* A. E. Porsild, *A. frieseana* subsp. *alaskana, A. media, A. monocephala,* and *A. nordhagiana* (Bayer 1987); and (3) hybridization among *A. aromatica, A. frie-*

seana subsp. *alaskana, A. media, A. monocephala,* and *A. nordhagiana* (Bayer and Stebbins 1987). I believe the *A. alpina* polyploid complex is rooted in hybridization events between *A. dioica* and *A. frieseana* subsp. *alaskana.*

R. T. Porsild (1914) concluded that *Antennaria alpina* was an old species, and that *A. glabrata* was a young species that developed from it. The distribution of *A. glabrata, A. porsildii,* and *A. ungavensis* led A. E. Porsild (1965) to conclude that they were not of recent hybrid origin, at least pre-Pleistocene time. Bayer (1990b) stated that polyploid agamic complexes such as *A. alpina* were the most recent to evolve because they were derived from the sexual progenitors of section *Catipes.* I agree with the statement of Rune and Rönning (1956) that *A. nordhagiana* and *A. porsildii* are parallel derivatives (both being glabrous) from *A. dioica* and *A. alpina,* respectively.

In summary, not only does *Antennaria alpina s.l.* occur in North America, but so do its three subspecies. The best characters to use to distinguish among the subspecies are the degree and distribution of pubescence on the surfaces of the basal leaves (see key). In subsp. *alpina* the leaves are glabrous on the adaxial surface and villous or tomentose on the abaxial; in subsp. *canescens* the leaves are villous or tomentose on both surfaces; in subsp. *porsildii* the leaves are entirely glabrous.

TAXONOMIC TREATMENT

1. Plants with well-developed, prostrate or ascending stolons, abaxial surface of basal leaves villous-tomentose ..... (2)
    2. Basal leaves glabrous on the adaxial surface .... 1. *A. alpina* subsp. *alpina*
    2. Basal leaves villous-tomentose on the adaxial surface .... 2. *A. alpina* subsp. *canescens*
1. Plants with poorly developed, erect or suberect stolons, abaxial surface of basal leaves glabrous .... 3. *A. alpina* subsp. *porsildii*

1. **Antennaria alpina** (L.) Gaertner subsp. **alpina,** De Fruct. Sem. Pl. 2: 410. 1791.

Gnaphalium alpinum L., Sp. Pl. 850. 1753. *Antennaria alpina* var. *typica* Fernald, Rhodora 26: 98. 1924; BASIONYM: *Gnaphalium alpinum.* TYPE: LAPLAND. No. 71—see Malte (1934) for discussion on this typification (LINN—microfiche!).

Antennaria alpina (L.) Gaertner var. *ungavensis* Fernald, Rhodora 18: 238. 1916. *A. ungavensis* (Fernald) M. O. Malte, Rhodora 36: 110. 1934; TYPE: CANADA. Ungava (Labrador): Stillwater River, 12 Aug 1896, *Spreadborough Geol. Surv. Can. no. 44442* (HOLOTYPE: GH!; ISOTYPE: CAN 105999!).

Antennaria arenicola M. O. Malte, Rhodora 36: 110. 1934. TYPE: CANADA. Quebec: east coast of Hudson Bay, Port Harrison, 58°17′N, 78°10′W, 18–20 Aug 1928, *Malte 120714* (HOLOTYPE: CAN 105983!; ISOTYPE: CAN 105982!).

Humifuse; stolons usually obvious, up to 10 cm long; basal leaves spathulate-oblanceolate, green, glabrous adaxially and villous-tomentose abaxially, 10–16 mm long, 2–4 mm wide; peduncle typically <18 cm long, bearing 7–12 peduncular leaves, middlemost 11–19 mm long, 1.4–2.4 mm wide, middle to distal tipped with a flat, oblong, scarious appendage; capitula 3–7 in corymb, 5–7 (8) mm long; phyllaries narrow, linear-lanceolate, acute, green, brown, black, or olivaceous, outermost 3–5 mm long, 0.9–1.3 mm wide, innermost longer, comparatively narrower, 5–6.4 mm long, 0.6–0.8 mm wide; corolla 3.5–4.7 (5) mm long; style 4.3–5.7 mm long; pappus bristles 4.6–6.2 mm long; cypselae brown, commonly glabrous, occasionally papillate, 0.7–1.6 mm long. Chromosome number determinations reported for the species (some under synonyms) from North America and Europe range between $2n = 56$ and 112 (Bayer 1984, 1990a; Bayer and Stebbins 1981, 1987; Chinnappa 1986; Chmielewski and Chinnappa 1988b, c, 1990; Halliday 1976; Lid 1963, as cited in Porsild 1965). Unless the actual specimen for which a chromosome number determination has been made is available for viewing, determinations as they pertain to specific taxa should, however, be considered with caution (i.e., I don't know which, if any, of the reports are from specimens belonging to my circumscription of subsp. *alpina*).

DISTRIBUTION AND HABITAT. *Antennaria alpina* subsp. *alpina* occurs on gravel, shale, or talus slopes, rocky schist cliffs, and wet or dry meadows to the alpine zone in western and eastern North America, Greenland, Scandinavia, and possibly to northwest Russia (Figure 3).

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA: Banff National Park, Sulphur Mtn., 22 Jul 1891, *Macoun 73013* (CAN); BRITISH COLUMBIA: Paradise Mine, ca. 15 mi west of Windermere, 31 Jul 1953, *Calder & Savile 11262*

(DAO); LABRADOR: Torngat Region, Kikkertasoak Island, Saglek Bay, 9 Aug 1926, *Woodworth 412* (CAN); NORTHWEST TERRITORIES: Franklin District, Baffin Island, Frobisher Bay, Ogac Lake, head of Ney Harbour, 5 Aug 1965 *McLaren 79* (CAN); QUEBEC: Fort Chimo, 11 Jul 1948, *Rousseau 44* (CAN).

Greenland. Godtchaab District, Ameralik Fjord, 64°07′N and 51°08′W, 20 Jul 1941, *Porsild 8200* (CAN).

Norway. Slopes of Oksfjellet east side of Tverelva River, 20 Jul 1968, *Alho & Kause* (DAO).

Sweden. Torne Lappmark, Karsovagge Valley, 17 Jun 1957, *Ray 26* (DAO); near Bjorkliden, 29 Jul 1950, *Moldenke & Moldenke 21046* (DAO).

2. **Antennaria alpina** (L.) Gaertner subsp. **canescens** (Lange) Chmielewski *comb. et stat. nov.*

Antennaria alpina var. *canescens* Lange, Flora Danica XLVII. tab. 2786, fig. 1. 1869. *A. canescens* (Lange) M. O. Malte, Rhodora 36: 109. 1934. *A. canescens* subsp. *canescens* [autonym generated by *A. canescens* subsp. *porsildii* (E. Ekman) Löve and Löve, Bot. Not. 128: 519. 1976]. In principle, the plants depicted in Flora Danica tab. 2786 were drawn in nature. Thus, the drawings are the type specimens, and consequently none were cited in the protologue. In C is a sheet which includes three collections numbered 1, 2, 3. The specimen designated as number 3 bears a striking resemblance to the type drawing and in my estimation is one and the same. TYPE: GREENLAND. District Colon. Godthaab: Jul–Aug, *Vahl s.n.* (LECTOTYPE: C!—here designated).

Antennaria canescens f. *fastigiata* Böcher, Arbejd. Dansk. Arkt. Sta. Disko 38: 33. 1963. TYPE: GREENLAND. Holsteinsborg (Mount Praestefjeldet), 66°56′N and 53°40′W, 18 Jul 1958, *Böcher 623* (HOLOTYPE: C!).

Antennaria alpina var. *cana* Fernald & Wiegand, Rhodora 13: 24. 1911. *A. cana* (Fernald & Wiegand) Fernald, Rhodora 18: 236. 1916. TYPE: CANADA. Newfoundland: Pointe Riche, 4 Aug 1910, *Fernald & Wiegand 4139* (HOLOTYPE: GH!; ISOTYPE: CAN 106057!).

Antennaria sornborgeri Fernald, Rhodora 18: 237. 1916. TYPE: CANADA. Labrador: Rama, 20–24 Aug 1897, *Sornborger 156* (HOLOTYPE: GH!).

Antennaria vexillifera Fernald, Rhodora 26: 99. 1924. TYPE: CANADA. Quebec: Matane County, between Mt. Mattaouisse and Mt. Collins, 8 Jul 1923, *Fernald, Griscom, Mackenzie, Pease, & Smith 26056* (HOLOTYPE: GH!; ISOTYPES: MT!, CAN 106056!).

Antennaria alpina f. *latifolia* E. Ekman, Svensk Bot. Tidskr. 21: 50. 1927. TYPE: GREENLAND. Umanak, 25–30 Aug 1923, *Ekman s.n.* (LECTOTYPE: S!—here designated).

Antennaria glabrata (J. Vahl) Greene f. *tomentosa* E. Ekman, Svensk Bot. Tidskr. 21: 51, pl. 1, figs. 3, 9. 1927. *A. hudsonica* M. O. Malte, Rhodora 36: 116. 1934. TYPE: GREENLAND. Narssak near Nord-Pröven, ca. 72°23′N. Type collections cited to be at C could not be located (Fredskild, pers. comm.). Inclusion of this form in subsp. *canescens* is based on the description which indicates that the rosette leaves are lanate-tomentose abaxially.

Antennaria longii Fernald, Rhodora 28: 237. 1927. TYPE: CANADA. Newfoundland: Pistolet Bay, Schooner (Brandy) Island, 18 Jul 1925, *Pease & Long 29177* (HOLOTYPE: GH!).

Antennaria brevistyla Fernald, Rhodora 33: 323. 1931. TYPE: GREENLAND. S. Disko, Nuk ost for Marraq, 69°25′N, 13 Aug 1929, *Porsild s.n.* (HOLOTYPE: GH!; ISOTYPE: CAN 450374!).

Antennaria columnaris Fernald, Rhodora 35: 331. 1933. TYPE: CANADA. Newfoundland: Gargamelle Cove, 20 Jul 1929, *Fernald, Long, & Fogg, Jr. 2076* (HOLOTYPE: GH!; ISOTYPE: MT!).

Antennaria confusa Fernald, Rhodora 35: 338. 1933. TYPE: CANADA. Newfoundland: Old Port au Choix, 21 Jul 1929, *Fernald, Long, & Fogg, Jr. 2078* (HOLOTYPE: GH!; ISOTYPE: MT!).

Antennaria atriceps Fernald ex Raup, Contr. Arnold Arb. 6: 207, pl. 8, fig. 2. 1934. TYPE: CANADA. British Columbia: west and northwest slopes of Mt. Selwyn, 56°1′N and 123°39′W, near small lake, elevation 5000 ft, 26 Jul 1932, *Raup & Abbe 4134* (LECTOTYPE: CAN 105927!—here designated; ISOLECTOTYPE: CAN 506917!).

Antennaria congesta M. O. Malte, Rhodora 36: 114. 1934. TYPE: CANADA. Quebec: Port Burwell, Hudson Strait, 60°22′N and 64°50′W, 25–28 Jul 1928, *Malte 120118* (HOLOTYPE: CAN 105922!). This name was previously placed in synonymy with *A. monocephala* subsp. *angustata* (Chmielewski and Chinnappa 1991).

Antennaria subcanescens Ostenfeld ex M. O. Malte, Rhodora 36: 112. 1934. TYPE: CANADA. Northwest Territories: Mackenzie District, Bernard Harbour, 68°47′N and 114°46′W, 14 Aug 1915, *Johansen 91546* (HOLOTYPE: CAN 106127!; ISOTYPE: GH!).

Antennaria canescens var. *pseudoporsildii* Böcher, Meddel. Gronl. 148(3): 32, fig. 9. 1963. *A. boecheriana* A. E. Porsild, Bot. Tidsskr. 61: 36. 1965. TYPE: GREENLAND. Kangerdlvarssuk Ikamiut, 65°48′N, 1958, *Böcher 270.* Although the type collection was cited as being in C it could not be located (Fredskild, pers. comm.). Because new rosette leaves of var. *pseudoporsildii* are initially hairy (these are lost with age), the taxon is included in subsp. *canescens.*

Stolons well developed, prostrate or ascending, up to 10 cm long; basal leaves spathulate-oblanceolate, permanently whitened both adaxially and abaxially with a silvery tomentum, 7–15 mm long, 2–4 mm wide; peduncle typically <12 cm long, bearing up to 10 linear peduncular leaves, middlemost 8–14 mm long, 1–2 mm wide, middle to distal tipped with a flat, oblong, scarious appendage; capitula 3–6 in corymb, 5–6.4 mm long; phyllaries linear-lanceolate, acute, green-black tipped, outermost 3–5 mm long, 0.8–1.4 mm wide, innermost longer, comparatively narrower, 4.8–6 mm long, 0.5–0.9 mm wide; corolla 3.2–4.2 mm long;

style 3.8–5.0 mm long; pappus bristles 4.5–5.5 mm long; cypselae brown, not papillate, 0.7–1.4 mm long. Chromosome number determinations for Greenland populations of $2n = 63$ (Jorgensen et al. 1958) are supplemented with North American $2n = 56$ (Chmielewski 1995c) and $2n = 70$ (Chmielewski and Chinnappa 1988d) counts.

DISTRIBUTION AND HABITAT. *Antennaria alpina* subsp. *canescens* occurs on various substrates, including granitic outcrops, gravel river beds, limestone gravel beds, and sand embankments in Scandinavia, coastal Greenland, Labrador, the Hudson Bay region, southern Baffin Island, west through the Canadian and Alaskan Arctic and south through the Rocky Mountains to Wyoming (Figure 4).

REPRESENTATIVE SPECIMENS: **Canada.** ALBERTA: Jasper National Park, near summit of Mt. Edith Cavell trail, 4 Aug 1989, *Chmielewski & Chmielewski CC4889* (UAC)—Note: Collections CC2135, CC2136, and CC2717 reported by Chmielewski and Chinnappa (1988b) as *A. stolonifera* A. E. Porsild better represent subsp. *canescens* and are treated as such here; LABRADOR: Crater Lake, North Hebron River valley, ca. 52 mi west southwest of Hebron, 58°02′N and 64°02′W, 26 Jul 1954, *Gillett 8648* (DAO); NEWFOUNDLAND: Region of St. John Bay, Eastern Point, 26 Jul 1919, *Fernald, Long, & Fogg, Jr. 2085* (MT); NORTHWEST TERRITORIES: Franklin District, Baffin Island, Frobisher Bay, Ogac Lake, 15 Aug 1962, *McLaren 7* (CAN); Keewatin District, Yathkyed or Hikolikdjuak Lake on the Kazan River, 62°30′N and 97°–98°30′W, 1–15 Aug 1930, *Porsild 5854* (CAN); Mackenzie District, Desperation Lake, 62°35′N and 112°15′W, 8 Jul 1961, *Scotter 1051* (DAO); QUEBEC: Wakeman Bay, 60°N and 70°W, Aug 1937, *Dutilly 4016* (CM); YUKON TERRITORY: Itsi Range, unnamed lake, 62°57′N and 130°09′W, 31 Jul–2 Aug 1960, *Calder & Kukkonen 27655* (DAO).

Greenland. Nugsuak Peninsula, Kingigtok, 70°10′N, 21 Jul 1928, *Erlanson 3288* (DAO).

Norway. Dovre, Opland, Fokstuen, 23 Jun 1939, *Osterlind* (DAO).

Sweden. Lapland, Tornetrask District, Jukkasjarvi Parish, Mt. Paddos, 68°–68°34′N and 18°–20°30′E, 12 Jul 1952, *Alm 1508* (DAO).

United States. ALASKA: 3 mi north of Okpilak Lake, 69°27′N and 153°58′W, 26 Jul 1958, *Cantlon & Malcolm 58-0391* (CAN); MONTANA: Flathead County, Glacier National Park, southeast of Gem Lake, 4 Aug 1987, *Lesica 4469* (MONTU); WASHINGTON: Whatcom County, Chowder Ridge, 7 mi southeast of Glacier, 31 Jul 1972, *Douglas & Douglas 4289* (DAO); WYOMING: Carbon County, Medicine Bow Range, between Lake Marie and Silver Lake, 5 Aug 1966, *Porter & Porter 10268* (CAS).

3. ***Antennaria alpina*** (L.) Gaertner subsp. ***porsildii*** (E. Ekman) Chmielewski *comb. nov.*

Antennaria porsildii E. Ekman, Svensk Bot. Tidskr. 21: 51, pl. 1, figs. 10, 11. 1927. *A. alpina* var. *porsildii* Sorensen, Meddel. Gronl. 101(3): 89. 1933. *A. canescens* (Lange) M. O. Malte subsp. *porsildii* (E. Ekman) Löve & Löve, Bot. Not. 128: 519. 1976. TYPE: GREENLAND. Danmarks Insel, ca. 70°30′N, Aug 1892, *Hartz s.n.* (HOLOTYPE: C!).

Antennaria alpina var. *glabrata* J. Vahl, Flora Danica XLVII. tab. 2786, fig. 4. 1869. *A. glabrata* (J. Vahl) Greene, Pittonia 3: 285. 1898. In principle, the plants depicted in Flora Danica tab. 2786 were drawn in nature. Thus, the drawings are the type specimens, and consequently none were cited in the protologue. In C is a sheet which at one time presumably consisted of two collections. Collection number 1 is missing, but collection number 2 bears a striking resemblance to the type drawing but is not exactly the same. The type drawing has three capitula and five roots, whereas the specimen per se has only two capitula and no obvious roots. I suspect that these have been lost as a consequence of handling. Further, the collection from insula Disco is labelled Dette Expl. Benyttet til Flora Danica (this specimen used for Flora Danica). TYPE: GREENLAND. Disco, Jul–Aug, *Vahl s.n.* (LECTOTYPE: C!—here designated).

Antennaria glabrata f. *ramosa* A. E. Porsild, Meddel. Gronl. 58: 181. 1926. TYPE: GREENLAND. Patut, 70°14′N, 8 Aug 1921, *Porsild s.n.* The type collection believed to be at C could not be located (Fredskild, pers. comm.). However, a single collection in CAN fits the protologue. (LECTOTYPE: CAN 281573!—here designated).

Antennaria porsildii f. *roseola* E. Ekman, Svensk Bot. Tidskr. 21: 52. 1927. TYPE: GREENLAND (presumably, as no specimen was cited). This form presumably differs from subsp. *porsildii* only in its pale red versus olivaceous-brown phyllaries.

Stolons short, suberect; basal leaves spathulate-linear or oblanceolate, glabrous, 9–16.5 mm long, 2–3 mm wide; peduncle slender, 4–8 cm long, bearing 4–8 linear peduncular leaves, middlemost 10–13.5 mm long and 1.2–1.8 mm wide, middle to distal tipped with a flat, oblong, scarious appendage; 1 or 2–4 capitula, 5.5–6.7 mm long; phyllaries oblong-lanceolate, acute, green-black tipped, outermost 4–5.5 mm long, 1–1.5 mm wide, innermost longer, comparatively narrower, 5.4–6.5 mm long, 0.7–0.9 mm wide; corolla 3.8–5.8 mm long; style 4.2–5.0 mm long; pappus 5.0–5.8 mm long; cypselae brown, not papillate, 0.9–1.3 mm long. Chromosome number determinations for Greenland and Scandinavian specimens (as *A. porsildii*) included $2n = 63$, 84 (Böcher 1950; Jorgensen et al. 1958) and $2n = 63$ (Nygren 1950; Lid 1963), respectively.

DISTRIBUTION AND HABITAT. *Antennaria alpina* subsp. *porsildii* occurs in dry rocky places among grasses or on fertile slopes at lower elevations (<700 m) in western Greenland as well as eastern arctic Canada (Figure 5).

REPRESENTATIVE SPECIMENS: **Canada.** NORTHWEST TERRITORIES: Franklin District, Baffin Island, Cape Searle, 67°10′N and 62°30′W, 16–17 Aug 1950, *Wynne-Edwards 9146* (CAN).

Greenland. Arveprinsens Ejland, Kangerdlo, northeast of Ata, 69°47′N, 50°52′W, 3 Aug 1981, *Fredskild 489* (DAO); Disko, Artisk Station, 69°15′N, 31 Aug 1925, *Porsild s.n.* (GH); Svartenhuk Halvo, Umivik, 71°38′N, 18 Jul 1929, *Porsild & Porsild s.n.* (GH); Ameragdla, northwest of Kilaersarfik, 18 Jul 1984, *Fredskild 84-115* (DAO); Isortoq, Holsteinsborg, Aug 1832, *J. Vahl s.n.* (C).

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ACHENE MORPHOLOGY, PRODUCTION AND GERMINATION, AND POTENTIAL FOR WATER DISPERSAL IN *BOLTONIA DECURRENS* (DECURRENT FALSE ASTER), A THREATENED FLOODPLAIN SPECIES

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ABSTRACT. The decurrent false aster, *Boltonia decurrens* (Asteraceae), is a Federally listed, threatened floodplain species endemic to a 400 km reach of the lower Illinois River and adjacent areas of the Mississippi River. The present study was conducted in response to the Recovery Plan for *B. decurrens,* which called for life history studies to provide information essential to planning management programs for the species. A series of laboratory studies was conducted to determine achene morphology, achene production and germination under a variety of conditions, and the potential for dispersal by water. *Boltonia decurrens* produces ca. 50,000 achenes per individual, and based on achene viability observed in this study, an average plant is capable of producing ca. 40,000 seedlings under optimal conditions for germination. There was no difference between germination of achenes produced by ray and disk florets; however, achene size had a significant effect on germination and viability, with larger achenes having higher levels of both. Achenes are morphologically adapted for flotation, and germination was not significantly reduced in achenes floated for four weeks. Achenes which were not exposed to light did not germinate, whether they were covered with aluminum foil or with sediment. Results suggest that factors other than fecundity are responsible for the threatened status of *B. decurrens.* Heavy siltation of river water caused by agricultural runoff, and flood control measures limiting dispersal may have contributed to the decline of the species.

Key Words: life history, threatened species, management, floodplain

The decurrent false aster, *Boltonia decurrens* (Torr. and Gray) Wood (Asteraceae), a Federally listed, threatened floodplain species (U.S. Fish and Wildlife Service 1988), occurs along a 400 km section of the lower Illinois River and nearby parts of the Mississippi River (Schwegman and Nyboer 1985; U.S. Fish and Wildlife Service 1990). *Boltonia decurrens* is an early successional species that requires either natural or human disturbance to create and maintain suitable habitat. Its natural habitat was wet prairies, shallow marshes, and shores of open rivers, creeks, and lakes (Schwegman and Nyboer 1985). In the past, the annual flood/drought cycle of the Illinois River provided the natural disturbance required by this species. Annual spring flooding created open, high-light habitat and reduced competition by killing other, less flood-tolerant, early successional species. Field observations indicate that in "weedy" areas without disturbance, the species is eliminated by competition within three to five years (U.S. Fish and Wildlife Service 1990). *Boltonia decurrens* has high light requirements for growth and achene germination (Smith et al. 1993; Smith et al. 1995), and shading from other vegetation is thought to contribute to its decline in undisturbed areas.

Boltonia decurrens also exhibits morphological adaptations for life on the floodplain. Stoecker et al. (1995) found *B. decurrens* to be extremely tolerant when maintained under conditions of root-zone saturation. All plants in the flood treatment survived to study completion at 56 days. The formation of aerenchyma, a common plant adaptation to flooding which allows diffusion of oxygen from aerial shoots to maintain root metabolism (Armstrong 1971; Crawford 1978; Laan et al. 1990), was extensive, increasing in adventitious roots from 26% of root cross section area in non-flooded plants to 49% in flooded plants (Stoecker et al. 1995).

Boltonia decurrens reproduces vegetatively and sexually. Vegetative production of one or more basal rosettes occurs during the fall. Rosettes bolt the following spring; plants flower and set achenes from late August to early October. Field monitoring by Schwegman and Nyboer (1985) suggested prolific achene production. Fall seedlings overwinter, and bolt and flower the following spring and summer. Spring seedlings, however, may either bolt and flower the same year or overwinter as small rosettes which bolt and flower the following year (Smith 1991). In areas where seedling production is low or nonexistent, *B. decurrens* populations can be maintained by basal rosette production. In fact, few seedlings are found in established populations (Moss 1997; Smith 1991). Seedling establishment is expected to be low due to the small achene size, the high light and temperature requirements for germination, and specific soil texture and microtopography requirements for germination and seedling growth (Baskin and Baskin 1988; Smith et al. 1995). The present study was conducted to determine the potential fecundity of *B. decurrens* and to examine the adaptive life history characteristics which enhance achene dispersal and survival on the floodplain.

MATERIALS AND METHODS

All achenes and plants used in this study were collected from a population near the Melvin Price Locks and Dam, St. Charles County, Missouri (lat. 38°52′06″N, long. 90°12′22″W; elev. 140 m). The height of 85 plants, every third plant along a transect, was measured and plants numbered on 12 Oct 1989. Eighty of the marked plants were collected on 2 Nov 1989, and transported to SIUE where total biomass was measured and inflorescences counted. Achenes for all germination experiments were collected on 3 Nov 1989.

Potential fecundity. Inflorescences on each plant were counted, and achenes per inflorescence were counted for a random subsample of 100 inflorescences. Potential fecundity was calculated as the average number of achenes per inflorescence × number of inflorescences for each plant. Shoots and roots were separated, dried at 80°C for four days, and then weighed. Correlations were calculated by the method of least squares (Sokal and Rohlf 1981) using Sigma Stat 2.0 (Jandel Scientific Software, San Rafael, CA), and the coefficient of correlation and statistical significance determined for the following combination of paired, random variables: plant height and potential fecundity (achene number per plant); total dry weight and potential fecundity; above ground dry weight and potential fecundity; and root dry weight and potential fecundity.

Germination of ray and disk achenes. A dissecting microscope (at 25×) was used to examine 100 inflorescences to determine the ratio of ray flowers to disk flowers and to compare achene mass, size, and morphology. Mass of each achene type was determined by weighing 200 of each on a Sartorius (Model L 420D) balance and calculating the mean weight per achene. Size (length, width, and height) of ten of each type of achene was measured using a dissecting microscope and a mm ruler. Three hundred achenes (30 achenes × 10 dishes) of each type were placed on filter paper in plastic petri dishes, soaked with deionized water, sealed in ZipLoc bags and placed at a randomly assigned position in a Conviron E-15 environmental chamber at 25°C, 75% relative humidity, 900 μMol m^{-2} s^{-1} Photon Flux Density and 12/12 h day/night cycle. For four weeks, at weekly intervals, achene germination was determined by emergence of the radicle. Statistical difference in germination between the two types was analyzed using Fisher's Exact Test (Sokal and Rohlf 1981). Statistical differences were inferred when $P < 0.05$. In addition, mass of each achene type was determined by weighing 200 of each and calculating the average weight per achene.

Size-related achene germination. A random sample of achenes was selected and separated into two size classes using a 0.5 mm screen filter (U.S.A. standard testing sieve, Fisher Scientific Co.). Six hundred large and 600 small achenes were separated into 12 lots of 100 each and placed on filter paper in petri dishes. To test for germination, six lots of 100 were incubated in deionized water only and the remaining six lots were treated with 0.5% tetrazolium chloride to determine viable, but dormant, achenes (Zhang and Maun 1989). All achenes were maintained in the environmental chamber, at conditions previously described, for three weeks. At the beginning of week 4, temperature in all treatments was raised to 35°C. All results were tested for significant differences (germination and viability) between the two size classes using Fisher's Exact Test (Sokal and Rohlf 1981).

Germination in darkness. Four replicate lots of 100 achenes each were randomly selected, placed on filter paper in plastic petri dishes, and soaked with deionized water. The petri dishes were wrapped in two layers of aluminum foil and placed in the environmental growth chamber for four weeks, with conditions as described above.

Germination of sediment covered achenes. Soil from the study population site was cleaned of large roots and rocks and sterilized. A 1.5 cm layer of sterile Promix potting soil was placed in 10 cm^2 pots and topped with 3.5 cm of sterilized site soil. This mixture was saturated with deionized water, 50 achenes placed in each pot, and covered with a layer of "silt" (site soil that had been mixed with deionized water in a Waring blender until it was the consistency of river silt). Four pots were used per treatment, with achenes placed at each of the following depths of silt: 0 cm (exposed), 0.5 cm, 1.0 cm, 1.5 cm, 2.0 cm, and 2.5 cm. Pots were placed in trays, watered, and covered with plastic wrap to retard the formation of a hard surface film. All treatments were maintained in the environmental growth chamber for four weeks, with conditions as previously noted. Germination was determined by emergence of hypocotyl and primary leaves.

Flotation and germination of achenes. One hundred disk achenes each were placed in three 250 ml Erlenmeyer flasks filled with 150 ml deionized water. Achenes were gently washed down from the sides of the flask once weekly with a pipette. At the end of the third week, one flask was placed on a shaker table for one week to simulate possible wave action. The number of floating achenes was counted weekly, and at the end of week 4 the achenes were placed on filter paper in plastic petri dishes, soaked with deionized water, sealed in ZipLoc bags and placed in an environmental growth chamber, with conditions as previously noted. Statistical difference in germination between the two treatments was analyzed using Fisher's Exact Test (Sokal and Rohlf 1981). Statistical differences were inferred when $P < 0.05$.

RESULTS

Potential fecundity. Plant height, biomass, and achene production were highly variable in this naturally occurring population (Table 1). Data analysis indicated positive correlations between inflorescence production and shoot dry weight ($r = 0.97$), root dry weight ($r = 0.94$), total dry weight ($r = 0.97$), and shoot height ($r = 0.88$; Table 2). Potential fecundity of the average whole plant (inflorescences/whole plant × achenes/inflorescence) was 51,121, or 26,923 for the mean individual shoot (inflorescences/individual shoot × achenes/inflorescence).

Germination of ray and disk achenes. Examination of inflorescences revealed that ray and disk flowers are morphologically distinct: disk flowers are perfect (bisexual), fertile, and yellow; ray flowers are pistillate, fertile, and vary from white to pink or pale purple. Both flower types appear to set seed routinely, producing achenes that differ significantly in size (Table 3). In addition, disk achenes have two prominent, stiff bristles emerging

Table 1. Plant height, dry weight (g DWT), and achene production for individual shoots and whole plants of *Boltonia decurrens.* * Root systems produced variable numbers of shoots. Each individual shoot was measured for height, dry weight, and achene production. ** Mean height, dry weight, and achene production were calculated for the shoots associated with each root system.

Character	Mean	SD	n
*Shoot height/individual (cm)	107.3	39.1	142
**Total shoot height/whole plant (cm)	204.1	210.2	80
Above-ground biomass/shoot (g DWT)	11.3	14.6	142
Above-ground biomass/whole plant (g DWT)	24.5	67.3	80
Root biomass (g DWT)	4.6	5.2	80
Total biomass/whole plant (g DWT)	29.1	75.3	80
Inflorescences/individual shoot	109.4	121.9	
Inflorescences/whole plant	207.8	367.9	
Achenes/inflorescence	247.4	49.3	100

from the base of the achene (remnant of the pappus). During flotation experiments, these bristles were observed to have small air bubbles clinging to them. The disk to ray flower ratio (4.3:1) was consistent in both large and small inflorescences. At this ratio, the number of each type of achene produced by an "average" plant (Table 1) would be ca. 41,475 disk achenes and 9645 ray achenes. Percent germination did not differ significantly between achene types.

Size-related germination and viability. Achene size had a significant effect on germination and viability (Table 4), with larger achenes having significantly greater ($P < 0.05$) percentages of both germination and viability. Viability of both size classes was significantly greater ($P < 0.001$) than germination. The effect

Table 2. Correlation coefficient (r) for Shoot Dry Weight (SDWT), Root Dry Weight (RDWT), Total Dry Weight (TDWT), and Shoot Height (HT) versus Number of Inflorescences (#INF) for individuals of *Boltonia decurrens* in the study. n = 80 for all parameters.

Characteristic	r	Significance (P-value)
SDWT × #INF	0.97	<0.001
RDWT × #INF	0.94	<0.001
TDWT × #INF	0.97	<0.001
HT × #INF	0.88	<0.001

Table 3. Number of disk and ray achenes per inflorescence; mass of both types; size (L = length, W = width, H = apical hair length); and percent germination. Sample sizes reflect numbers per each achene type. Values in rows with different letters (a,b) are significantly different ($P < 0.05$). Statistical differences for achene size were determined by Student's t test and for germination by Fisher's Exact Test. * Mass of each achene type was determined by weighing 203 achenes of each type and calculating the average. — Prominent hairs not present.

Characteristic	Disk Achenes	Ray Achenes	Sample Size
#/Inflorescence (SD)	223.4(44.5)^{a}	52.0(11.1)^{a}	100
*Mass ($g \times 10^{-5}$)	6.5	4.9	203
L (mm) (SD)	1.8 (0.1)^{a}	1.3 (0.1)^{b}	10
W (mm) (SD)	1.3 (0.1)^{b}	0.9 (0.1)^{b}	10
H (mm) (SD)	0.9 (0.2)	—	10
% Germination	62.1(12.2)^{a}	68.0(13.5)^{a}	300

of temperature on germination, however, was not statistically significant.

Germination in darkness. Of the 400 achenes in the dark treatment, one germinated (0.25%).

Germination of sediment covered achenes. Forty percent of the achenes placed on the sediment surface germinated during the 4-week observation period. With a single exception (1 achene at 1.0 cm sediment depth), no achenes germinated when covered with 0.5 to 2.5 cm of sediment (Table 5).

Table 4. Germination and viability in large and small achenes of *Boltonia decurrens* after 3 and 4 weeks. Figures in rows with different letters (a,b) are significantly different ($P < 0.001$) as determined by Fisher's Exact Test. *All values for comparisons among large vs. small achenes were significantly different ($P < 0.05$) as determined by Fisher's Exact Test. $n = 300$ for each experiment.

Achene Size	% Germination	% Viability
*Large (>0.5 mm)		
Week 3 (25°C)	37.6^{a}	77.6^{b}
Week 4 (35°C)	42.0^{a}	83.0^{b}
*Small (<0.5 mm)		
Week 3 (25°C)	29.3^{a}	69.3^{b}
Week 4 (35°C)	32.3^{a}	74.0^{b}

Table 5. Germination of achenes of *Boltonia decurrens* located on the soil surface or buried under one of five depths (0.5 cm, 1.0 cm, 1.5 cm, 2.0 cm, and 2.5 cm) of silt for 4 weeks. n = 200 for each treatment.

Siltation Depth (cm)	% Germination
0	40
0.5	0
1.0	0.5
1.5	0
2.0	0
2.5	0

Flotation and germination of achenes. The percent germination of achenes which had been floated for 4 weeks was within the range observed in other portions of the study (Tables 4, 5, and 6). Three achenes (1.5%) germinated while still in the water. There was a significant reduction ($P < 0.001$) in the number of achenes floating after 4 weeks that had been shaken (to simulate wave action) when compared to those floating on still water. There was no significant difference ($P < 0.051$) in percent germination of achenes in still water when compared to achenes that were shaken to simulate wave action.

DISCUSSION

Boltonia decurrens is a prolific achene-producer with a potential fecundity of an average of ca. 50,000 achenes per mature individual. Comparisons of inflorescence production with shoot dry weight, root dry weight, total dry weight, and shoot height indicate that larger, more robust plants produce more achenes. This may be an important consideration in natural populations, because there are two distinctive size groups of individuals: flowering plants produced from vegetative rosettes, which are large

Table 6. Flotation and germination for achenes of *Boltonia decurrens* after 4 weeks in deionized water in laboratory flasks. Figures in columns with different letters (a,b) are significantly different ($P < 0.05$) as determined by Fisher's Exact Test. *Includes 3 achenes which germinated while floating.

Treatment	% Floating	% Germination	n
Stationary Flask	71^a	*47	200
Shaken Flask	20^b	39	100

(1–2 m), and flowering individuals produced from spring-germinated seedlings, which are often less than 0.75 m in height (M.S., pers. obs.). Populations established in the first year following a severe flood are composed solely of seedling-derived flowering plants; however, populations in the second year of succession, or in areas where a disturbance wasn't severe enough to eliminate all previous plants, are composed of a mixture of plant types. The population in the present study was composed of a mixture of both flowering types. To determine reproductive potential of any single population in any given year, the composition of the population must be assessed in terms of the two reproductive types of flowering individuals.

It is clear from the results of this study that larger achenes have higher germinability and viability than smaller achenes (Table 4). The test for embryo viability indicated that many achenes remained viable, but dormant, under the light and temperature regimes used in this study. If dormancy were broken by an optimal temperature regime or cold stratification (Baskin and Baskin 1988), percent germination could potentially have risen from ca. 39% to ca. 79%.

Achenes of *Boltonia decurrens* often germinate in the fall, before stratification occurs; therefore, the potential exists for significant seedling establishment during fall and early winter. Estimating an initial germination of 39% of all freshly produced achenes, one could project a mean production of ca. 20,000 seedlings per average plant in the fall. Recent studies in our laboratory (Moss 1997), however, indicate that seedling mortality in the field was extremely high (99.99%) for fall and early winter seedlings at Horseshoe Lake, Madison County, Illinois, during 1995 and 1996.

Under warmer spring and summer temperatures, the remaining 40% of the total achene crop could germinate, providing an additional 20,000 seedlings per plant. In 1995, a year in which flood waters inundated the Horseshoe Lake area until late June, Moss (1997) reported 0.1% survival for spring and summer seedlings, resulting in the production of ca. 20 seedlings per average individual which had flowered the previous fall. Seedling production and survival undoubtedly depend heavily on site conditions, and seedling establishment would vary between years and among sites. This information may help explain the extremely large fluctuations known to occur in population sizes between years (U.S. Fish and Wildlife Service 1990).

An examination of sediment characteristics of Illinois River Valley soil and the sediment load and transparency of flood waters suggests some potential insights into the threatened status of *Boltonia decurrens.* Lee and Stall (1976a) made theoretical calculations of the annual sediment loss in the Illinois River Basin of 25 million metric tons (mmt) or 3.34 mt/ha. About 11 mmt of sediment are annually transported out of the Illinois Valley to the Mississippi River at Grafton, leaving 14 mmt deposited in the water areas and certain unleveed areas of the floodplain. Most transport of sediment occurs during high discharge (Lee and Bhowmik 1979). By removing about half of the floodplain from inundation by the river, drainage and levee districts have increased flood heights and the deposition of sediments on the remaining lakes and unleveed floodplain of the Illinois Valley (Bellrose et al. 1979, 1983). Lee and Stall (1976a) found that sediments deposited in the Illinois River Valley were made up almost equally of silt and clay particles with insignificant amounts of sand.

The present study of *Boltonia decurrens* demonstrated that achenes will not germinate in the dark. Of the 400 achenes in foil-covered dishes, only one germinated. Although one might infer that 0.25% of the achenes of *B. decurrens* will germinate in the dark, these results were more likely caused by a pinpoint of light penetrating the aluminum foil covering the petri dishes (by the end of the study, several very small holes had developed along creases in the foil). In addition, achenes which were covered with as little as 0.5 cm of sediment did not germinate; therefore, if achenes are deposited by flood waters and subsequently covered by a shallow layer of sediment, it is unlikely they will germinate. Natural or human disturbance of the soil, exposing the achenes to light, would be required for germination. This inference is consistent with the recent historical restriction of populations of *B. decurrens* to human-disturbed, agricultural settings (Schwegman and Nyboer 1985).

Sediment type may also be an important factor in achene germination and long-term survival of populations. *Boltonia decurrens* populations have been observed growing on a variety of soil types (Schwegman and Nyboer 1985; Smith 1991); however, laboratory studies (Smith et al. 1995) comparing achene germination and growth on two soil types, silty clay (6.7% sand, 53.3% silt, and 40% clay) and loamy sand (80% sand, 16.7% silt, and 3.3% clay) indicate that germination and seedling growth were significantly greater on sand than on clay. These laboratory results suggest that the silt and clay sediment being deposited by flood events (Lee and Stall 1976b) is not ideal for germination and growth. Soil type may thus be important in determining the distribution pattern of this species.

Water clarity may affect survival and growth of both seedlings and basal rosettes. Achenes of *Boltonia decurrens* are capable of germination in both fall and spring (Moss 1997; Smith 1991). If germination is followed by a flood which reduces water clarity for an extended time period, the new seedlings, even if not washed away (Moss 1997), will likely die due to lack of adequate light for growth (Smith et al. 1993, 1995). Basal rosettes have been observed (M.S. and T.M.K., pers. obs.) to bolt and grow under water when the water was clear, with plants emerging above the water surface and subsequently flowering. This has not been observed in turbid flood waters of the Illinois River. The high light requirements of *B. decurrens* (Smith et al. 1993) would not be met under turbid flood waters.

Achenes of *Boltonia decurrens* are morphologically structured for flotation, and therefore, presumably are adapted for dispersal on river currents. The hairs which emerge from the base of the disk achene trap and hold an air bubble, and the light, thin, broad achene is easily borne on water surfaces. In this study, there was no significant difference in percent germination of achenes which had been floated for 4 weeks and those in other portions of the study, and 20% of achenes floated under condition of simulated wave action were still floating after four weeks. These data indicate that achenes of *B. decurrens* have the potential for long distance dispersal on water.

In the field, there is indirect evidence of dispersal by water. *Boltonia decurrens* has been observed growing in a series of windrows, parallel to the shoreline at Meredosia Lake and Smith Lake, Cass and Morgan Counties, respectively, Illinois (T.M.K. and M.S., pers. obs.). Achenes were deposited on the shoreline by wind-generated waves, and the observed distribution pattern resulted from separate dispersal events as the lake water level receded after flooding. Such observations demonstrate that water dispersal occurs under natural conditions.

Although achenes are apparently adapted for water dispersal, much of the Illinois River Valley is isolated from the river by drainage and levee districts. The levee systems provide an effective barrier to achene dispersal landward of the levee system, except during major floods when the levees are overtopped. In essence, suitable habitat for the species is unavailable because of the levee systems.

The effect of the failure of the species to disperse freely to recently flooded areas is compounded by its apparent inability to compete with other vegetation as succession progresses (Schwegman and Nyboer 1985; Smith et al. 1993). Populations isolated landward of the levee do not experience the annual flood/drought cycle that is necessary to eliminate species which compete for light and suitable germination sites. Without periodic reduction of competing vegetation, *Boltonia decurrens* does not persist for more than five years at any one site.

Studies of basic life history characteristics of threatened and endangered species are necessary to understand the circumstances contributing to their status. While it is impossible to re-create the floodplain system that supported such species, it is possible that knowledge of factors critical to their survival will enable agencies to prevent their extinction through the formulation and implementation of well-designed management plans. The feasibility of substituting alternative site disturbance such as disking, mowing, burning, or controlled flooding should be investigated to determine if it is possible to successfully manage *Boltonia decurrens,* and therefore, to reverse the current population decline.

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NOTE

REDISCOVERY, STATUS, AND PRESERVATION OF THE ENDANGERED KANKAKEE GLOBE MALLOW (*ILIAMNA REMOTA*) IN INDIANA

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Iliamna remota Greene [formerly *Sphaeralcea acerifolia* Nutt., *S. remota* (Greene) Fernald, and *Phymosia remota* (Greene) Britton] was first discovered by E. J. Hill, growing on a small, gravelly island (Langham Island) in the Kankakee River near Altorf, Illinois, on June 29, 1872 (Sherff 1946; Strausbaugh and Core 1932). This island is, presumably, the only naturally occurring locality for *I. remota*. The phytogeographic origins of this exclusive, natural population are unknown.

On July 4, 1944, Dr. S. W. Witmer of Goshen College found four colonies of the species growing "2 miles east of New Paris, Elkhart County, Indiana" (*S. W. Witmer s.n.*, F 68972). The plants were found at a site where the railroad crosses the Elkhart River (Figure 1).

In addition to the disjunct Indiana population, another colony of *Iliamna remota* was found on June 28, 1964, near Glen Wilton, Virginia, where U.S. 220 crosses the Chesapeake & Ohio Railroad and the James River (Keener 1964). Another Virginia locality for *Iliamna* was found by J. H. Browning on Peters Mountain at Narrows, Virginia (*E. E. Sherff s.n.*, F). These specimens, however, are considered by some to be separate species (*I. corei* Sherff). According to Sherff (1949), the species are distinguished by the fact that the flowers of *I. remota* are fragrant and those of *I. corei* are not (suggesting chemical differences). The morphology of the leaves of the two taxa is also somewhat different. The blades of *I. corei* are narrower and have a "terminal lobe oblong or subcuneately narrowed below and subtended with sharp sinuses," whereas the leaves of *I. remota* are broader with shallower, less pronounced sinuses (Sherff 1946).

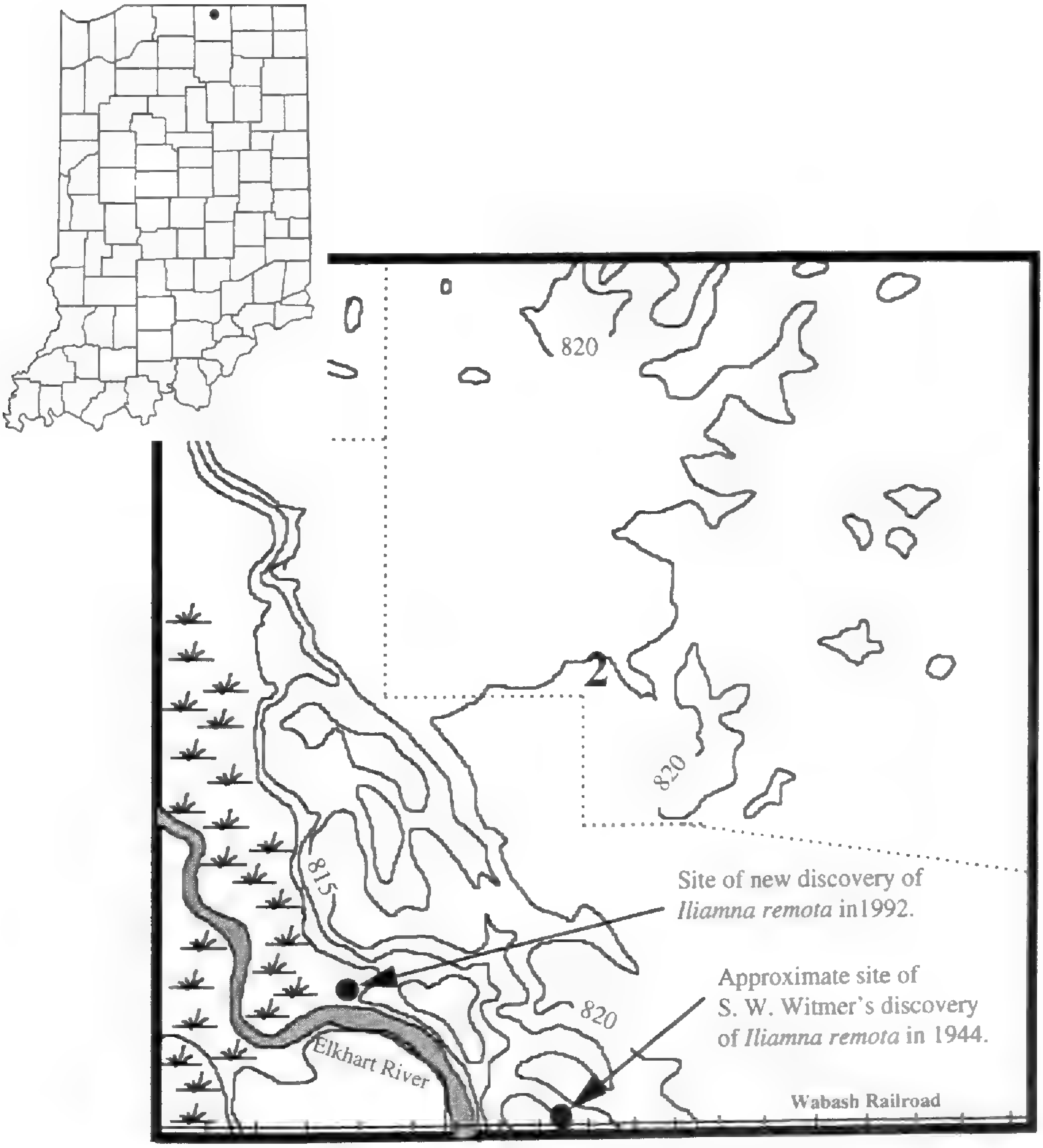

Figure 1. Map of Section 2, T35N, R6E, Elkhart County, Indiana, showing the location of historic (1944) and extant colonies of *Iliamna remota.*

The origins of the Indiana and Virginia populations of *Iliamna remota* are apparently anthropogenic. According to Sherff (1949) the Wildflower Preservation Society of Chicago (circa 1919), recognizing that *Iliamna* was in danger of extinction because of its isolation, obtained a liberal quantity of seeds from Langham Island and scattered them far and wide, perhaps from windows of moving trains, in the hope of spreading the species. The presence of both the Indiana and Virginia stands near railroads seems to substantiate this.

Although *Iliamna remota* is listed as Endangered in the state of Indiana, it is curiously and inexplicably absent from the U.S. Federal Register of endangered plants.

NATURAL HABITAT OF *ILIAMNA REMOTA*

The only known natural population of *Iliamna remota,* on Langham Island, is, geologically, a relatively recent establishment. The island occurs within the glaciated region created by the Laurentide Ice Sheet of Wisconsin age. The late-glacial Kankakee Flood, circa 15,000 yrs. BP, would have been the last major geologic disturbance, and the plants must have become established sometime after this event (Schwegman 1984). Schwegman (1984) suggests two possible origins of the plant: 1) it originated from migrants of other species [belonging to the genera *Iliamna* or *Sphaeralcea*] from the Rocky Mountains that speciated rather quickly in response to different environmental conditions, or 2) it may have been transported to the area from cultivars derived by American Indians.

The natural habitat of *Iliamna* is partially to fully open areas with a well drained, often gravel substrate, harboring woodland and prairie herbs (but lacking coarse grasses), with a sparse scattering of bur oak (*Quercus macrocarpa*), red oak (*Q. rubra*), and bitternut hickory (*Carya cordiformis*). It thrives in savannas, old fields, or where frequent natural disturbances (e.g., fire, erosion, ice-scour, wind-throws) push back succession and hinder the growth of high shrubs. Schwegman (1991) provides a detailed account of the flora, history, and physiography of the type locality.

Although the disjunct populations of *Iliamna remota* may be a result of human activity, they should be regarded as significant populations worthy of protection. Seeds of the species may have been spread throughout the railroad and highway corridors in the east, but the only known places where they became established were in two sites: one in Indiana and one in Virginia. These feral populations, because of their apparent habitat specificity, provide insight into the natural history of the species.

STATUS AND PRESERVATION OF THE INDIANA POPULATION

Original site of discovery. An attempt to preserve the Indiana locality resulted in a lease agreement between the Indiana chapter of The Nature Conservancy and the railroad company. A parcel of land surrounding the *Iliamna* was set aside as The Kankakee Mallow Nature Preserve. Lack of management of invasive vegetation at the site reduced the *Iliamna* population until July 4, 1988, when it was reported extirpated at the site (Paul T. Slabaugh, pers. comm.). Careful inspection of the site by the authors in 1992 resulted in the same conclusion.

Discovery of a new colony. On August 7, 1992, seven colonies were found outside of the original preserve (*M. E. Jacobs s.n.,* F 2112195). These colonies were growing along the border of a cornfield 312 m north of the Elkhart River railroad bridge and about 600 m from the site of the original colonies of *Iliamna* reported by S. W. Witmer in 1944. Seeds from these new colonies were collected by the primary author for studies on germination. All seeds that were neither frozen nor scarified with a scalpel did not germinate, six percent of seeds which were frozen but not scarified germinated, sixty-nine percent of seeds subjected to scarification without freezing germinated, and ninety-four percent of seeds subjected to both freezing and scarification germinated. The seed coat remained tenaciously around the cotyledons of germinating seeds and required physical removal. This suggests that a more thorough reduction in the strength of the seed coat is required for natural germination. John E. Schwegman (pers. comm.), formerly of the Illinois Department of Conservation, has found that fire is needed to scarify seeds so they will germinate in the wild. Baskin and Baskin (1997) also reported the need for physical scarification or fire (in *I. corei,* at least), but found that no seeds germinated as a result of freezing alone (compare to 6% germination in the *I. remota* seeds from Indiana).

Evidence has shown that many Malvaceae seeds are viable for as long as 40 years (Hill 1982a, b). Baskin and Baskin (1997) report that seeds of *Iliamna corei* (a close relative of *I. remota*) remained viable for more than three years. Seeds from the Elkhart County *I. remota* were determined to remain viable for at least four years, as germination of the seeds collected from the new locality in 1993 was successful as of summer, 1997. The resulting plants produced seed in the first season.

Rediscovery of Witmer's colony. In the late summer of 1993, two living stems from the original Witmer site, 219 m east of the east end of the railroad bridge, were rediscovered on gravel in a tangle of *Hypericum perforatum, Daucus carota,* and *Prunus padus* (all of which are exotic species in Indiana). Seeds from this original locality were collected, germinated, and cultivated in the garden of M. E. Jacobs, Goshen, Indiana (early accounts of *Iliamna* in cultivation are given by Wadmond 1932). In the fall of 1993, the two stems at the Witmer locality were destroyed by farming operations. In an effort to preserve the original feral population, mature specimens from the germinated seeds in Jacobs's garden were transplanted to property owned by The Friends of the Pumpkinvine Nature Trail in an area along the abandoned corridor of the Pumpkinvine Railroad in a sunny spot between State Road 4 and the entry gate of the trail (south side of trail).

RECOMMENDATIONS

While it is very fortunate that the Indiana population of *Iliamna remota* has managed to survive for almost 80 years, it is clear that management will be required to insure its long term survival and viability at the site. Lack of management and education of local residents in the past has almost led to the demise of this unique plant existing in a locality with significant historical and ecological value. Transplants made to private properties managed by interested and knowledgeable botanical enthusiasts have saved the population at least momentarily, but carefully guided management (including periodic, local burning), as well as educational outreach by recognized state and national organizations, will be a more long term assurance of the survival of the population. Ecological and molecular research, including DNA analysis of the three main populations in the U.S., is recommended for the future.

ACKNOWLEDGMENTS. The authors would like to thank Dr. Steven R. Hill of the Illinois Natural History Survey for helpful comments on the manuscript. Steve Gangsloff, Elkhart County Parks and Recreation Department, helped establish the new *Iliamna* preserve and is also charged with its maintenance.

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BOOK REVIEW

The European Garden Flora. Vol. V. Dicotyledons (Part III): Limnanthaceae to Oleaceae edited by an Editorial Committee, J. Cullen, Chairman. 1997. xviii + 646 pp. illus. ISBN 0-521-42096-2 $155.00 (hardback). Cambridge University Press, Melbourne, Australia.

This book is the fifth of six in a project sponsored by the Royal Botanical Garden, Edinburgh, The Royal Horticultural Society, London, and the Stanley Smith Horticultural Trust, Cambridge. The objective is to provide a professional taxonomic treatment of woody and herbaceous plants cultivated for amenity in Europe that is useful for the informed amateur gardener. The flora is based on original taxonomic studies to provide a scientific foundation for accurate identification and determination of correct names and synonyms of plants in cultivation. It reflects plant names currently cited in catalogues, horticultural works, and the nursery and landscape industries. A number of authorities contributed generic treatments following a format, vocabulary, and guidelines defined and edited by an editorial committee (Royal Botanic Garden, Edinburgh; University Botanical Garden, Cambridge; Royal Horticultural Society's Garden, Wisley; National Botanic Gardens, Glasnevin, Dublin; Natural History Museum, London; Liverpool Museum; University of Reading). The project treats about 300,000 species arranged in about 11,000 genera in about 400 families.

Horticultural references include both exotic and native plants, typically arranged artificially (i.e., alphabetical; growth form). Cultivated plants often exhibit morphological features not found in wild plants due to environmental pressures of cultivation and/or selection processes and cultural practices of man. Therefore, identification of an unknown plant found in cultivation is difficult, even for professionals.

The European Garden Flora is an excellent reference used frequently as compared to most standard horticultural references that lack most of the following attributes. First, plants are arranged taxonomically, not artificially. Related taxa occur together for easy comparison. Second, there are dichotomous keys (to families, genera, and species) to guide the reader in identification of unknowns or confusing taxa. Couplets are parallel in construction, avoid ambiguous terms (e.g., otherwise, not as above) and present contrasting characters. Diagnostic keys are provided for some larger genera. Third, descriptions are full and diagnostic, and more consistent in parallel construction as compared to many references, providing one with better comparisons of taxa. Descriptions are followed by a short paragraph documenting the number of taxa, world distribution, and horticultural information (e.g., propagation, maintenance, economic aspects, taxonomic problems). Larger genera are supported by illustrations (line drawings, leaf prints); these are limited, but excellent identification tools when used. Fourth, notes are provided on common misapplication of names and problems in classification and nomenclature that are unresolved currently. Literature citations are included to point readers to sources (revisions, inventories) with more in-depth information. Fifth, the glossary includes simplified terminology to aid amateurs, as well as line drawings of typical vegetative and reproductive features to supplement the text.

The European Garden Flora is an exciting reference with a large inventory of plants in cultivation, current taxonomic data, correct names and synonyms, and identification aids. It is technical, yet the format is "user friendly" for both amateurs and professionals. The extensive index, guide words at the top of the page (i.e., family name and genus) and each new taxon in boldface type make it easy for one to locate taxa. The cost may appear high initially, but the set is a bargain when one considers the current and authoritative information, keys, quality illustrations, guides to additional literature sources, and low cost per page. *The European Garden Flora* will be used frequently; therefore, it's a "must" reference for personal and institutional libraries.

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BOOK REVIEW

Weeds of the Northeast by Richard H. Uva, Joseph C. Neal, and Joseph M. DiTomaso. 1997. 397 pp. illus. line drawings and color photos. ISBN 0-8014-3391-6 $60.00 (hardcover); 0-8014-8334-4 $29.95 (softcover). Comstock Publishing Associates, Ithaca, NY.

This recent publication is an outstanding identification and information guide to "weeds" of the northeastern United States and southern Canada. It includes 299 species, of which about 160 are treated in detail. The authors define "weed" fairly broadly, and include a wide range of nonaquatic ruderals. The book's focus is on herbaceous species, but it includes some shrubs and vines, and ten common species of hardwood tree seedlings likely to occur in disturbed habitats. The species covered include both exotic and native ruderals (*Aster pilosus, Toxicodendron radicans, Smilax rotundifolia*), but the book omits a number of what may be considered noxious weeds in natural or even agricultural settings (*Rhamnus frangula* or *Juncus effusus*) while including species of less concern (*Rhus typhina, Juncus tenuis*) to conservation land managers.

The book provides a substantial amount of useful information for each of the species covered in detail. A full page of descriptive information includes common names, general description, propagation strategies, phenology, descriptions of seedlings, mature plants, flowers and fruits, postsenescence appearance, habitat, and descriptions of similar species. A full page of color photographs includes habit, seedlings, seeds, infloresences, and similar species. The book includes excellent line drawings of vegetative structures for 29 species of grasses, sedges, and rushes, although the photos of these are less successful than for the dicots.

Identification aids include keys which lead to groups of from one to 15 species. There is a series of shortcut identification tables that also lead to groups of species. The reader must turn to the full description for each of the species in the group in order to complete the identification. Clear comparative tables at the end of the book provide easy multicharacter matrices that distinguish species in difficult groups, among others, the pigweeds and amaranths, the umbels, trifoliate legumes, sowthistles and prickly lettuces, and common weedy grasses (based on vegetative characters).

This will be a useful book for agriculturalists, horticulturalists, land managers, and amateur and professional botanists who seek an easy and thorough guide to the ruderal flora of the Northeast. The keys, descriptions, and photographs emphasize common names rather than scientific (although there are some odd conventions—"eveningprimrose" as one word) and vegetative characteristics rather than flowers, and are presented simply and clearly. The comparative tables are straightforward and nontechnical. The photos, particularly of seeds and seedlings, provide information not found in other plant identification guides, and will be very useful to field ecologists.

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NEBC MEETING NEWS

November 1997. Dr. Stephen Spongberg of the Arnold Arboretum spoke on the topic "New Plants in Yankee Soils—An Abbreviated History of Plant Introduction from Eastern Asia." Steve began with an overview of the floristic diversity and complexity of eastern Asia. China, while roughly the same size as the continental U.S. and at the same latitudes, contains three times the diversity of vascular plants, with a reported flora of over 30,000 species. The natural floristic relationships between eastern Asia and eastern North America were noted first by Linnaeus in 1750 and were rediscovered independently by Asa Gray a century later. Steve's topic, however, was the history of eastern Asian natives now cultivated in North America—a history influenced by religion, politics, and commerce more than by science.

Introductions from eastern Asia began in the 1750s, when the Dutch were able to import seeds of Ginkgo from China, where the tree existed only in cultivation on temple grounds. Jesuit missionaries, allowed to establish a mission in Beijing, sent back *Sophora japonica, Koelreuteria,* and *Ailanthus,* presumably with good intentions. After the end of the Opium Wars in 1842, when China's treaty ports opened to foreigners, the Horticultural Society of London sent Robert Fortune to seek botanical novelties. Although limited to the treaty ports and Chinese garden flora, Fortune was responsible for the introduction of numerous Asian cultivars of *Chrysanthemum, Camellia,* peonies, and the ubiquitous *Dicentra spectabilis,* as well as woody ornamentals including *Hydrangea paniculata.*

A Bavarian physician and botanist, Philipp von Siebold, was responsible for collecting a tremendous number of Japanese plants, despite being confined to the Dutch trading settlement on the island of Deshima. With George Rodgers Hall, a Harvard-trained doctor, he successfully introduced *Malus floribunda, Rosa rugosa, Rhododendron brachycarpum, Magnolia sieboldii, Wisteria floribunda, Taxus cuspidata,* and *Lilium auratum.* Hall's garden, still intact at his home in Bristol, Rhode Island, contains his original plant of *Taxus* brought back from Japan in 1865.

The British nurseryman, James Veitch, began to send collectors to China in the late 1800s, most successfully Ernest Wilson. Wilson was the first to collect live material of *Davidia involucrata* and, on his second expedition, *Meconopsis integrifolia.* Charles

Sargent visited Japan in 1892 and successfully introduced *Malus sargentii, Prunus sargentii,* and *Rhododendron kaempferi.* In 1905, Sargent hired Wilson and sent him to China, Japan, and Korea on a series of collecting expeditions. Wilson's accessions included *Forsythia ovata, Corylopsis, Magnolia sargentii, Cornus kousa, Kolkwitzia, Stewartia, Acer griseum,* and *Lilium regale.* Wilson's collecting career ended with a severely broken leg, although this adventure resulted in his being the only botanist known to have been featured in *Ripley's Believe It or Not.*

The most recent eastern Asian introduction is *Metasequoia glyptostroboides,* the "dawn redwood," collected by Elmer Merrill, Director of the Arnold Arboretum, almost exactly fifty years ago, on January 3, 1948. Following Merrill's expedition, China essentially became closed to foreigners again until after Nixon re-established relations. The first joint Sino-American Botanical Expedition was held in 1980, and this collaboration continues with preparation of the first *Flora of China.*

December 1997. Dr. Harlan Banks spoke on "Sixty Years with Devonian Plants," an enthusiastic review of his more than 60-year-long romance with the early vascular plants of the Devonian. During the evening, Dr. Banks took the Club on a whirlwind tour of the people, places, and fossil plants that have contributed to our current understanding of the early land plant record.

The early land plants underwent a rapid and remarkable evolutionary radiation in the period from 400 to 350 million years ago, and developed two major lineages early in the Devonian—the Psilopsida (leafless plants with terminal sporangia) and the Zosterophyllopsida. Dr. Banks's primary work has contributed to making sense of this diversification, particularly with the zosterophylls, the early ancestors of the lycopods. These plants had simple leaves with single, unbranched vascular strands, sporangia on the upper surface of the leaves, and a unique xylem structure, and probably looked much like *Lycopodium selago.*

The plants provide a fascinating view of diversity, and Dr. Banks shared the thrill of each new discovery: the 3-forked leaves of *Colpodexylon* (formerly thought to be spines); *Leclerqia,* with its uniquely distinctive 5-forked leaves; other taxa with curved, falcate leaves with broad deltoid bases; *Sawdonia,* from the Gaspé, the first of these plants demonstrated to have stomates on the leaves and sporangia borne directly on the sides of the stems; and

Psilophyton, from the Devonian of Wyoming, found to have clusters of terminal sporangia. The careful study of these plants has also provided evidence of Devonian arthropods, based on scars similar to those that result from modern chewing or sucking insects, and the earliest record of a spider based on fossil material trapped in the leaves of *Leclerqia.*

January 1998. Ten members stepped forward to share their slides and tales of botanical explorations throughout the world. George Newman traveled to the Bruce Peninsula of Ontario, and to a spectacular marl bog near Lake Huron, where *Pinguicula* covers acres. George also pursued *Sarracenia* in the Okefenokee Swamp, despite the occasional hazards of alligators and water moccasins. Don Lubin traveled no further than his yard in Allston, where he cultivates more than 30 species of ferns. Don brought ferns grown from spores to share with other Club members, and invited members to visit his garden if summer ever returns to New England. David Hunt confined his travels to New York state, but visited numerous unusual and unique communities in the Adirondacks and coastal oak forests. The sloping acidic fens which support alpine sedges and rare sphagnums, although below treeline, were perhaps the most intriguing of these communities. Paul Somers shared slides of the Club's June and September field trips, and unusual plants from the southern Appalachians. Pam Weatherbee visited southern Illinois, where floodplain forests, limestone outcrops, and rich woods support a wealth of spring-flowering species, including *Trillium flexipes, T. recurvatum,* and *Collinsia verna.*

The western United States was represented by Leila Schultz, who described testing a new GIS-based predictive model for rare species habitats and a new species richness map prepared for Utah. Field investigation of one locality predicted to contain rare species found that the model worked even better than anticipated, when the team discovered a new species of *Eriogonum*! Lisa Standley shared slides of the colorful flora of the East Mojave National Preserve in California, including Joshua trees and the spectacular Mojave mound cactus.

Three Club members traveled even further afield. Dorothy Andrews traveled up the Rio Negro from Manaus, observing life in and along the river. Unfortunately, Dorothy's trip coincided with an unusual prolonged drought, which resulted in few flowers, fruits, or birds along the river, and a complete absence of howler monkeys. Ray Angelo visited the Singapore Botanical Gardens, encountering kapok trees, orchids, and figs. Ray also demonstrated that he had successfully eaten durians. Barre Hellquist shared pictures from his sabbatical in Australia, including the vast opium fields of Tasmania. Barre focused on the newly discovered "Wollemi Pine," a species of *Araucaria* formerly known only from the fossil record, and recently found to occur in the Wollemi National Park north of Sydney, with a population of only 38 individuals.

February 1998. Barre Hellquist, of North Adams State College, spoke on "Aquatic Plants of Australian Billabongs, Gilgais, and Backwaters." Barre recently returned from a 6-month sabbatical at the Royal Botanical Gardens in Sydney, where he worked on the Flora of Australia project. Barre's research work in Australia focused on *Aponogeton,* a genus of (mostly) submerged tropical aquatics with broad, linear leaves and small, undistinguished flowers. Barre succeeded in complicating the Australian flora by turning the 4 known native species into 10 taxa, some of which are distinguished only by seed characters. In his travels through the wetlands of northern Australia (the billabongs and gilgais), Barre and various companions saw an incredible number of *Nymphaea* species: *macrosperma,* which has very large leaves and seeds, but tiny flowers; *pubescens,* the only night-bloomer; *violacea, immutabilis,* and *atrans,* which have blue or lavender outer petals and white inner petals; *ellenii,* a dwarf white flower; *rubra*; and *gigantea,* whose populations vary in flower color from lilac to pink and deep purple. *Nymphaea atrans* flowers undergo a spectacular color sequence, initially blue and white, aging to a deep pink.

Tropical Australia supports a wide diversity of aquatics. Barre introduced Club members to numerous species of *Nymphoides,* some with yellow flowers; *Caldesia,* a member of the Alismataceae with leaves that mimic water-lilies and fruits that mimic *Trapa; Monochoria,* a lovely purple-flowered genus related to *Pontederia; Ottelia,* a showy member of the Hydrocharitaceae, as well as the more familiar genera *Utricularia, Eriocaulon, Vallisneria, Triglochin* (some species look like *Vallisneria*), *Limosella,* and, of course, *Potamogeton.*

—LISA A. STANDLEY, Recording Secretary.

RHODORA, Vol. 100, No. 901, p. 96, 1998

IN MEMORIAM

REED C. ROLLINS
1911–1998

Reed C. Rollins, the Asa Gray Professor of Systematic Botany Emeritus at Harvard University, and director of the Gray Herbarium from 1948 to 1978, died April 28, He was 86.

Born in Lyman, Wyoming, Rollins graduated with honors from the University of Wyoming, received his master's degree from Washington State University, and his Ph.D. from Harvard in 1941. A member of the Society of Fellows from 1937 to 1940, he joined Harvard's Faculty of Arts and Sciences in 1948. He was a member of the National Academy of Sciences, The American Academy of Arts and Sciences, and many professional societies.

Before coming to Harvard, Rollins served as associate professor of biology at Stanford University and as a geneticist for the U.S. Department of Agriculture. He worked on the Emergency Guayule Rubber Research Project for the U.S.D.A. during World War II. His research covered many areas in taxonomy and genetics, but the primary focus of his work was on the mustard family, Brassicaceae.

He leaves his wife Kathryn; a daughter, Linda White, of Hingham, Massachusetts; a son, Richard, of Portland, Oregon; stepdaughters Sydney Roby of Baltimore, Maryland, and Helen Roby of Toronto, Ontario; a brother, Dr. S. P. Rollins of Phoenix, Arizona; a sister, Mrs. Allene Carter of Tulsa, Oklahoma; and five grandchildren.

A memorial service was held on May 22 in Appleton Chapel in the Memorial Church at Harvard University.

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Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

GENERAL: Manuscripts should be submitted in triplicate. The text must be double-spaced throughout, including tables, figure legends, and literature citations. Use a non-proportional font throughout and do not justify the right margin. Do not indicate the style of type through the use of capitals, underscoring, or bold, except for names of genera and species which should be in italics or underscored throughout. Do not underline punctuation. All pages should be numbered in the upper right-hand corner. For guidance in matters not addressed here, consult the editorial office by phone at (603) 862-3205, FAX (603) 862-4757, or e-mail: janets@christa.unh.edu. Brevity is urged for all submissions. Submit manuscripts to the Editor-in-Chief.

TITLE, AUTHOR(S), AND ADDRESS(ES): Center title, in capital letters. Omit authors of scientific names. Below title, include author(s) name(s), affiliation(s), and address(es). If "current address" is different, it should follow immediately below, not as a footnote.

ABSTRACT: An abstract and a list of key words should be included with each paper, except for shorter papers submitted as Notes. An abstract must be one paragraph, and should not include literature citations or taxonomic authorities. Please be concise, while including information about the paper's intent, materials and methods, results, and significance of findings.

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FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad distribution. Keys and synonymy for systematic revisions should be prepared in the style of "A Monograph of the Genus *Malvastrum*," S. R. Hill, RHODORA 84: 159–264, 1982. Designation of a new taxon should carry a Latin diagnosis (rather than a full Latin description), which sets forth succinctly how the new taxon differs from its congeners.

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THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
Cambridge, MA 02138

The New England Botanical Club is a nonprofit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, and has a large herbarium of New England plants and a library. It publishes a quarterly journal, RHODORA, which is now in its 100th year and contains about 400 pages per volume. Visit our web site at http://www.herbaria.harvard.edu/nebc/

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ATLAS OF THE FLORA OF NEW ENGLAND: POACEAE

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ABSTRACT. Dot maps are provided to depict the distribution at the county level of the Poaceae growing outside of cultivation in the six New England states of the northeastern United States. The 338 taxa (species, subspecies, varieties, and hybrids, but not forms) are mapped based on specimens in the major herbaria of Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut, with primary emphasis on the holdings of the New England Botanical Club herbarium (NEBC). Brief synonymy to account for names used in recent manuals and floras for the area, habitat, chromosome information, and common names are also provided.

Key Words: flora, New England, atlas, distribution, Poaceae

This article is the second in a series that will present the distributions of the vascular flora of New England in the form of dot distribution maps at the county level. The atlas is being posted on the internet at http://www.herbaria.harvard.edu/~rangelo/Neatlas0/WebIntro.html where we will attempt to keep it updated.

This work encompasses all vascular plants (pteridophytes and spermatophytes) at the rank of species, subspecies, and variety growing outside of cultivation in the six New England states (Figure 1). Hybrids are also included, but forms and other ranks below the level of variety are not. The dots are based primarily on voucher specimens in the herbaria of New England representing reproducing populations, or plants persisting long after cultivation when it is uncertain that they are actually naturalized. This second installment comprises the Poaceae. The number of taxa treated is 341, of which 338 are mapped; 152, a remarkably high 45 percent, are not native to New England, and 6 are hybrids. Future accounts will treat the distribution of the rest of the angiosperms.

We intend to gather this series of articles, together with additional background material, into a separate volume upon completion of all the maps. It is our hope, in the meantime, that these articles will stimulate additional field work to supplement the distributions portrayed in the maps. The New England Botanical Club herbarium, which has proven to be the most important resource for this project, is especially eager to receive specimens documenting range extensions. We also would like to be informed of such specimens in other herbaria. Similarly, because the atlas of the New England flora will be continuously updated as new information becomes available, we are eager to receive notification of published corrections of cytological information and new, documented chromosome counts for taxa in the New England flora.

MATERIALS AND METHODS

Materials and methods are as outlined in Angelo and Boufford (1996) and are not repeated here.

TAXONOMY AND FORMAT

The taxonomy and nomenclature adopted for this work essentially follow that of a revision of A. Hitchcock and A. Chase's *Manual of the Grasses of the United States* (Barkworth et al., editors), except that genera are arranged alphabetically, as are species within genera. Named and unnamed hybrid taxa are placed alphabetically at the end of the genus. Unnamed hybrids combine the names of the progenitors alphabetically by epithet. Taxa that are not native to New England are indicated by uppercase text. A number of pending name changes (primarily in *Panicum*) could not be implemented since they were still unpublished at the time this work was sent to press.

Cited chromosome numbers are taken from indices prepared by Cave (1958a, b, 1959a, b, 1960, 1961, 1962, 1963, 1964, 1965), Goldblatt (1981, 1984, 1985, 1988), Goldblatt and Johnson (1990, 1991, 1994, 1996), Löve and Löve (1975), Moore (1973, 1974, 1977), and Ornduff (1967, 1968, 1969). Very few of the counts are based on material from New England, but instead reflect counts made from throughout the range of the taxon.

Synonymy is provided primarily with respect to names used in standard manuals covering New England published from 1950 onward, including Fernald (1950), Gleason (1952), Gleason and Cronquist (1991), Seymour (1982), and Hitchcock (1951).

The following list will aid readers in finding familiar names that have been transferred to other genera:

Agropyron (in part) ⇒ *Elymus, Pascopyrum*

Andropogon (in part) ⇒ *Schizachyrium*

Agrostis (in part) ⇒ *Apera*

Avena (in part) ⇒ *Avenula*

Deschampsia (in part) ⇒ *Vahlodea*

Diplachne ⇒ *Leptochloa*

Elymus (in part) ⇒ *Leymus, Taeniatherum*

Elytrigia ⇒ *Elymus, Pascopyrum*

Festuca (in part) ⇒ *Lolium, Vulpia*

Glyceria (in part) ⇒ *Torreyochloa*

Heleochloa ⇒ *Crypsis*

Helictotrichon ⇒ *Avenula*

Leptoloma ⇒ *Digitaria*

Oryzopsis ⇒ *Piptatherum*

Panicum (in part) ⇒ *Urochloa*

Pseudosasa ⇒ *Arundinaria*

Puccinellia (in part) ⇒ *Torreyochloa*

Scleropoa ⇒ *Desmazeria*

Stipa ⇒ *Piptochaetium*

Triodia ⇒ *Tridens*

Trisetum (in part) ⇒ *Sphenopholis*

The following are taxa reported from our area in manuals, but no specimens seen:

Agrostis verticillata (*Agrostis viridis, Polypogon viridis*)
Ammophila arenaria
Apera interrupta
Aristida longespica (typical)

Avena barbata
Briza maxima
Bromus rubens
Calamagrostis perplexa
Danthonia sericea
Elymus hispidus subsp. *barbulatus* (*Agropyron trichophorum*)
Elymus trachycaulus subsp. *subsecundus* (*Agropyron trachycaulum* vars. *ciliatum* and *unilaterale*)
Eragrostis hirsuta
Hordeum brachyantherum
Hordeum gussoneanum (*Hordeum hystrix*)
Leptochloa uninervia
Muhlenbergia ramulosa (*Sporobolus ramulosus*)
Poa interior (*P. nemoralis* subsp. *interior*)
Poa secunda (*P. nevadensis* of Hitchcock 1951)

ANGIOSPERMAE (MAGNOLIOPSIDA)—ANGIOSPERMS

MONOCOTYLEDONEAE (LILIIDAE)

POACEAE

Agropyron

AGROPYRON CRISTATUM (Linnaeus) Gaertner—Crested Wheatgrass (Figure 2). $2n$ = 14, 28, 42. Waste places. From Eurasia.

AGROPYRON DESERTORUM (Fischer ex Link) Schultes—(Figure 2). $2n$ = 14, 28. Waste places. From Eurasia.

Agrostis

AGROSTIS CANINA Linnaeus—Velvet Bent (Figure 2). $2n$ = 14, 16, 28, 35, 42, 56. Fields, meadows, hillsides. From Europe.

AGROSTIS CAPILLARIS Linnaeus—Rhode Island Bent (Figure 2). $2n$ = 28–35. Fields, pastures, roadsides, thickets, riverbanks. From Europe. [*A. TENUIS* Sibthorp; *A. TENUIS* var. *ARISTATA* (Parnell) Druce]

AGROSTIS ELLIOTTIANA Schultes—(Figure 3). 2*n* = 28. Fields, roadsides. From farther south.

AGROSTIS EXARATA Trinius—Spike Bent (Figure 3). 2*n* = 28, 42, 56. Clearings in woods along dirt roads. From western North America. [*A. EXARATA* var. *MONOLEPIS* (Torrey) Hitchcock]

AGROSTIS GIGANTEA Roth—Redtop (Figure 3). 2*n* = 28, 42. Riverbanks, meadows, fields, shores, moist places. From Europe. [*A. ALBA*—misapplied; *A. STOLONIFERA* Linnaeus var. *MAJOR* (Gaudin) Farwell]

Agrostis hyemalis (Walter) Britton, Sterns & Poggenburg—Ticklegrass (Figure 3). 2*n* = 14, 28, 42. Dry fields, open woods.

Agrostis mertensii Trinius—(Figure 4). 2*n* = 41, 42, 49, 50, 55, 56. Mountain ledges. [*A. borealis* Hartman; *A. borealis* var. *americana* (Scribner) Fernald]

Agrostis perennans (Walter) Tuckerman—Autumn Bent (Figure 4). 2*n* = 28, 42. Open woods, thickets, dryish open soil. [*A. perennans* var. *aestivalis* Vasey; *A. perennans* var. *elata* (Pursh) Hitchcock; *A. altissima* (Walter) Tuckerman]

Agrostis scabra Willdenow—Fly-away Grass (Figure 4). 2*n* = 28, ca. 35, 42. Roadsides, sterile, open soil (dry or wet). [*A. scabra* var. *geminata* (Trinius) Swallen; *A. scabra* var. *septentrionalis* Fernald; *A. geminata* Trinius; *A. hyemalis* (Walter) Britton, Sterns & Poggenburg var. *scabra* (Willdenow) H. L. Blomquist; *A. hyemalis* var. *tenuis* (Tuckerman) Gleason]

AGROSTIS STOLONIFERA Linnaeus—Creeping Bent (Figure 4). 2*n* = 24, 28–46. Shores, marshes, shallow water. From Europe. [*A. STOLONIFERA* var. *COMPACTA* Hartman; *A. STOLONIFERA* var. *PALUSTRIS* (Hudson) Farwell; *A. ALBA* Linnaeus var. *PALUSTRIS* (Hudson) Persoon; *A. PALUSTRIS* Hudson]

Aira

AIRA CARYOPHYLLEA Linnaeus var. *CARYOPHYLLEA*—Silver Hairgrass (Figure 5). 2*n* = 14, 28. Dry sand, waste places. From Europe.

AIRA PRAECOX Linnaeus—(Figure 5). 2*n* = 14. Sandy fields. From Europe.

Alopecurus

Alopecurus aequalis Sobolewski—(Figure 5). 2*n* = 14, 28. Shallow water, shores, meadows, ditches. [*A. aequalis* var. *natans* (Wahlenberg) Fernald]

ALOPECURUS CAROLINIANUS Walter—(Figure 5). 2*n* = 14, 28. Cultivated land. From farther west and south.

ALOPECURUS GENICULATUS Linnaeus—Marsh Foxtail (Figure 6). 2*n* = 14, 28. Wet roadsides, ditches, shallow water. From Eurasia.

ALOPECURUS MYOSUROIDES Hudson—Slender Foxtail (Figure 6). 2*n* = 14, 28. Fields, waste places. From Europe.

ALOPECURUS PRATENSIS Linnaeus—Meadow Foxtail (Figure 6). 2*n* = 28, 42. Fields, meadows, roadsides. From Eurasia.

Ammophila

Ammophila breviligulata Fernald—Beachgrass (Figure 6). 2*n* = 28. Sand dunes.

Ammophila champlainensis Seymour—Champlain Beachgrass (Figure 7). Shores of freshwater lakes.

Amphicarpum

AMPHICARPUM PURSHII Kunth—(Figure 7). 2*n* = 18. Roadsides. From farther south.

Andropogon

Andropogon gerardii Vitman—Big Bluestem (Figure 7). $2n$ = 20, 40, 60, 70, 80–86. Dry, open ground. [*A. gerardii* var. *chrysocomus* (Nash) Fernald]

Andropogon glomeratus (Walter) Britton, Sterns & Poggenburg—Bushy Beardgrass (Figure 7). $2n$ = 20. Boggy or other wet soils. [*A. virginicus* Linnaeus var. *abbreviatus* (Hackel) Fernald & Griscom]

Andropogon virginicus Linnaeus—Broom-sedge (Figure 8). $2n$ = 20. Dry, open soil, thin woods, upper shores of ponds.

Anthoxanthum

ANTHOXANTHUM ARISTATUM Boissier—(Figure 8). $2n$ = 10, 20. Waste places. From Europe. [*A. PUELII* Lecoq & Lamotte]

ANTHOXANTHUM ODORATUM Linnaeus—Sweet Vernal-grass (Figure 8). $2n$ = 10, 15, 20, 28. Fields, roadsides, woods, waste places. From Europe.

Apera

APERA SPICA-VENTI (Linnaeus) P. Beauvois—(Figure 8). $2n$ = 14. Waste places. From Europe. [*AGROSTIS SPICA-VENTI* Linnaeus]

Aristida

Aristida basiramea Engelmann ex Vasey—(Figure 9). Dry, sandy soil.

Aristida dichotoma Michaux—Poverty-grass (Figure 9). Dry, sterile soil. [*A. dichotoma* var. *curtissii* Gray ex S. Watson & Coulter; *A. basiramea* Engelmann ex Vasey var. *curtissii* (A. Gray) Shinners; *A. curtissii* (A. Gray) Nash]

Aristida longespica Poiret var. *geniculata* (Rafinesque) Fernald—(Figure 9). Sandy soil.

Aristida oligantha Michaux—Prairie Three-awn (Figure 9). $2n = 22$. Dry, open, sterile soil.

Aristida purpurascens Poiret—(Figure 10). Dry sandy or gravelly soil.

ARISTIDA PURPUREA Nuttall var. *NEALLEYI* (Vasey) Allred—(Figure 10). $2n = 22, 44$. Dry soil, roadsides. From farther west. [*A. GLAUCA* (Nees) Walpers]

Aristida tuberculosa Nuttall—Sea-beach Needlegrass (Figure 10). Dunes, dry sterile soil.

Arrhenatherum

ARRHENATHERUM ELATIUS (Linnaeus) P. Beauvois ex J. & C. Presl subsp. *ELATIUS*—Tall Oatgrass (Figure 10). $2n = 14, 28, 42, 56$. Fields, roadsides, waste ground. From Europe.

ARRHENATHERUM ELATIUS (Linnaeus) P. Beauvois ex J. & C. Presl subsp. *BULBOSUM* (Willdenow) Schübler & Martens—(Figure 11). $2n = 28$. Fields, roadsides, waste ground. From Europe. [*A. ELATIUS* var. *BULBOSUM* (Willdenow) Spenner]

Arthraxon

ARTHRAXON HISPIDUS (Thunberg) Makino—(Figure 11). $2n = 10, 36$. Damp roadsides, ditches, shores. From eastern Asia. [*A. HISPIDUS* var. *CRYPTATHERUS* (Hackel) Honda]

Arundinaria

ARUNDINARIA JAPONICA Siebold & Zuccarini ex Steudel—Arrow Bamboo (Figure 11). $2n = 48$. Woods, stream banks. From eastern Asia. [*PSEUDOSASA JAPONICA* (Siebold & Zuccarini ex Steudel) Makino ex Nakai]

Avena

AVENA FATUA Linnaeus—Wild Oat (Figure 11). $2n = 42$. Waste places. From Europe.

AVENA SATIVA Linnaeus—Oat (Figure 12). $2n$ = 20, 42. Waste places, roadsides. From Europe. [*A. SATIVA* var. *ORIENTALIS* (Schreber) Alefeld]

AVENA STRIGOSA Schreber—(Figure 12). $2n$ = 14, 28. From Europe.

Avenula

AVENULA PUBESCENS (Hudson) Dumort—(Figure 12). $2n$ = 14, 28. Fields, roadsides. From Europe. [*AVENA PUBESCENS* Hudson; *HELICTOTRICHON PUBESCENS* (Hudson) Pilger]

Beckmannia

BECKMANNIA SYZIGACHNE (Steudel) Fernald—Slough-grass. A specimen of this Asian species collected from Cumberland County, Maine, was noted in the Ahles notebooks as being in the University of Massachusetts (Amherst) herbarium, but the voucher cannot be found there.

Bouteloua

Bouteloua curtipendula (Michaux) Torrey—Tall Grama-grass (Figure 12). $2n$ = 20–103. Dry woods.

BOUTELOUA GRACILIS (Kunth) Lagasca ex Griffiths—Blue Grama-grass (Figure 13). $2n$ = 20–84. Waste areas. From farther west.

BOUTELOUA HIRSUTA Lagasca—Hairy Grama-grass (Figure 13). $2n$ = 12–50, ca. 60. Waste areas. From farther west.

BOUTELOUA REPENS (Kunth) Scribner & Merrill—Slender Grama-grass (Figure 13). $2n$ = 23, 40, 46, 60. Waste areas. From farther west and south. [*B. FILIFORMIS* (Fournier) Griffiths]

BOUTELOUA RIGIDISETA (Steudel) Hitchcock—(Figure 13). $2n$ = 40. Waste areas. From farther west and south.

BOUTELOUA SIMPLEX Lagasca—Mat Grama-grass (Figure 14). $2n = 20, 40$. Waste areas, wool waste. From farther west.

Brachyelytrum

Brachyelytrum erectum (Schreber ex Sprengel) P. Beauvois var. *erectum*—(Figure 14). $2n = 22$. Rich, moist woods and thickets.

Brachyelytrum erectum (Schreber ex Sprengel) P. Beauvois var. *glabratum* (Vasey ex Millspaugh) Koyama & Kawano—(Figure 14). $2n = 22$. Rich, moist woods and thickets. [*B. erectum* var. *septentrionale* Babel]

Brachypodium

BRACHYPODIUM PINNATUM (Linnaeus) P. Beauvois—(Figure 14). $2n = 18, 20, 28$. Waste areas. From Europe.

Briza

BRIZA MEDIA Linnaeus—(Figure 15). $2n = 10, 14, 28$. Roadsides, meadows, moist soil. From Europe.

BRIZA MINOR Linnaeus—(Figure 15). $2n = 10, 14$. Waste places. From Europe.

Bromus

BROMUS ARVENSIS Linnaeus—(Figure 15). $2n = 14$. Fields, roadsides. From Europe.

BROMUS BRIZIFORMIS Fischer & C. A. Meyer—Quake-grass (Figure 15). $2n = 14$. Roadsides, waste places. From Europe.

Bromus ciliatus Linnaeus—Fringed Brome (Figure 16). $2n = 14, 28, 56$. Rich, moist thickets. [*B. ciliatus* var. *intonsus* Fernald; *B. dudleyi* Fernald]

BROMUS COMMUTATUS Schrader—Hairy Chess (Figure 16).

$2n = 14, 28, 56$. Fields, roadsides, waste places. From Europe.

BROMUS ERECTUS Hudson—(Figure 16). $2n = 28–112$. Fields, roadsides. From Europe.

BROMUS HORDEACEUS Linnaeus subsp. *HORDEACEUS*—Soft Chess (Figure 16). $2n = 14, 28$. Fields, roadsides, waste places. From Europe. [*B. MOLLIS* Linnaeus]

BROMUS HORDEACEUS Linnaeus subsp. *PSEUDOTHOMINEI* (P. M. Smith) H. Scholz—(Figure 17). Low meadows, grasslands. From Europe. [*B. MOLLIS* Linnaeus forma *LEIOSTACHYS* (Hartman) Fernald]

BROMUS HORDEACEUS Linnaeus subsp. *THOMINEI* (Hardouin) Braun-Blanquet—(Figure 17). $2n = 28$. Waste places. From Europe. [*B. THOMINEI* Hardouin]

BROMUS INERMIS Leysser—Hungarian Brome (Figure 17). $2n = 28, 42, 54, 56, 70$. Fields, roadsides. From Europe. [*B. INERMIS* var. *DIVARICATUS* Rohlena]

BROMUS JAPONICUS Thunberg—Japanese Chess (Figure 17). $2n = 14, 28$. Waste places. From Eurasia. [*B. JAPONICUS* var. *PORRECTUS* Hackel]

Bromus kalmii A. Gray—(Figure 18). $2n = 14$. Basic soil in dry, rocky or sandy woods and thickets and in meadows.

Bromus latiglumis (Shear) Hitchcock—(Figure 18). $2n = 14$. Rich, alluvial woods and riverbanks. [*B. altissimus* Pursh; *B. purgans*—misapplied]

BROMUS LEPIDUS Holmberg—(Figure 18). $2n = 28$. Waste places. From the Old World.

BROMUS MARGINATUS Nees—(Figure 18). $2n = 42$. Waste places. From farther west. [*B. BREVIARISTATUS* Buckley; *B. CARINATUS*—misapplied]

Bromus pubescens Muhlenberg ex Willdenow—Canada Brome (Figure 19). $2n = 14$. Dry, open, woods in basic soil. [*B. purgans*—misapplied; *B. purgans* var. *laeviglumis* (Scribner) Swallen]

BROMUS RACEMOSUS Linnaeus—(Figure 19). $2n = 14, 28$. Waste places. From Europe.

BROMUS RIGIDUS Roth—Ripgut Grass (Figure 19). $2n = 28, 42, 56, 70$. Waste places, seaports. From Europe.

BROMUS SECALINUS Linnaeus—Cheat (Figure 19). $2n = 14, 28$. Fields, waste places, roadsides. From Europe.

BROMUS SQUARROSUS Linnaeus—(Figure 20). $2n = 14$. Waste places. From Europe.

BROMUS STERILIS Linnaeus—(Figure 20). $2n = 14, 28$. Waste places, roadsides. From Europe.

BROMUS TECTORUM Linnaeus—Downy Chess (Figure 20). $2n = 14, 28$. Fields, roadsides, waste places. From Europe.

Calamagrostis

Calamagrostis canadensis (Michaux) P. Beauvois var. *canadensis*—Bluejoint (Figure 20). $2n = 28, 42–66$. Meadows, shores, bogs, open swamps. [*C. canadensis* var. *robusta* Vasey]

Calamagrostis canadensis (Michaux) P. Beauvois var. *langsdorfii* (Link) Inman—(Figure 21). $2n = 28, 42, 56, 59$–ca. 64. High altitudes. [*C. canadensis* var. *scabra* (J. Presl) Hitchcock; *C. nubila* Louis-Marie]

Calamagrostis canadensis (Michaux) P. Beauvois var. *macouniana* (Vasey) Stebbins—(Figure 21). Open, moist, grassy areas.

Calamagrostis cinnoides (Muhlenberg) Barton—(Figure 21). Swamps, wet woods, damp sandy or peaty soils.

CALAMAGROSTIS EPIGEJOS (Linnaeus) Roth var. *GEORGICA* (K. Koch) Ledebour—(Figure 21). 2*n* = 28, 42, 56, 70. Fields, waste places. From Eurasia.

Calamagrostis pickeringii A. Gray—(Figure 22). 2*n* = 28. Bogs, peaty alpine soils, shores, riverbanks. [*C. pickeringii* var. *debilis* (Kearney) Fernald & Wiegand]

Calamagrostis stricta (Timm) Koeler subsp. *stricta*—(Figure 22). 2*n* = 28–126. Gravelly shores, riverbanks. [*C. neglecta* (Ehrhart) P. G. Gaertner, B. Meyer & Scherbius]

Calamagrostis stricta (Timm) Koeler subsp. *inexpansa* (A. Gray) C. W. Greene—Northern Reedgrass (Figure 22). 2*n* = 28, 56, 70, 84–120, 123. Wet ledges, ridgetop soils, gravelly shores, riverbanks, usually at high altitudes. [*C. fernaldii* Louis-Marie; *C. inexpansa* A. Gray; *C. inexpansa* var. *brevior* (Vasey) Stebbins; *C. inexpansa* var. *novae-angliae* Stebbins; *C. inexpansa* var. *robusta* (Vasey) Stebbins; *C. lacustris* (Kearney) Nash]

Cenchrus

Cenchrus longispinus (Hackel) Fernald—Field Sandbur (Figure 22). 2*n* = 34. Sandy fields, roadsides, railroads. [*C. pauciflorus*—misapplied]

CENCHRUS SPINIFEX Cavanilles—Coast Sandbur (Figure 23). 2*n* = 34. Sandy areas. From farther south. [*C. INCERTUS* M. A. Curtis]

CENCHRUS TRIBULOIDES Linnaeus—Dune Sandbur (Figure 23). 2*n* = 34. Coastal sands, especially dunes. From farther south.

Chloris

CHLORIS CUCULLATA Bischoff—(Figure 23). 2*n* = 40. Wool waste. From farther west.

CHLORIS GAYANA Kunth—Rhodes Grass (Figure 23). 2*n* = 20, 30, 40. Fields, waste places. From Africa.

CHLORIS VERTICILLATA Nuttall—Windmill Grass (Figure 24). $2n$ = ca. 28, 40, 63. Roadsides. From farther west.

CHLORIS VIRGATA Swartz—Feather Fingergrass (Figure 24). $2n = 20, 36, 40$. Wool waste. From tropical America.

Cinna

Cinna arundinacea Linnaeus—Common Woodreed (Figure 24). $2n = 28$. Wet woods, swamps.

Cinna latifolia (Treviranus ex Göppert) Grisebach—Drooping Woodreed (Figure 24). $2n = 28, 56$. Wet woods, thickets, recent clearings.

Corynephorus

CORYNEPHORUS CANESCENS (Linnaeus) P. Beauvois—Gray Hairgrass (Figure 25). $2n = 14$. Sandy fields, roadsides, barrens. From Europe.

Crypsis

CRYPSIS SCHOENOIDES (Linnaeus) Lambert—(Figure 25). $2n = 32, 36$. Waste places. From Europe. [*HELEOCHLOA SCHOENOIDES* (Linnaeus) Host ex Roemer]

Cynodon

CYNODON ARISTIGLUMIS Caro & E. A. Sánchez—(Figure 25). Waste areas. From South and Central America.

CYNODON DACTYLON (Linnaeus) Persoon—Bermuda Grass (Figure 25). $2n = 18, 27, 30, 36, 40, 54$. Waste places. From Europe.

Cynosurus

CYNOSURUS CRISTATUS Linnaeus—(Figure 26). $2n = 14$. Roadsides. From Europe.

Dactylis

DACTYLIS GLOMERATA Linnaeus—Orchard-grass (Figure 26). $2n = 14, 21, 28$. Roadsides, fields, orchards, waste places. From Europe. [*D. GLOMERATA* var. *CILIATA* Petermann; *D. GLOMERATA* var. *DETONSA* Fries]

Dactyloctenium

DACTYLOCTENIUM AEGYPTIUM (Linnaeus) Willdenow—Crowfoot-grass (Figure 26). $2n = 18–24, 27, 36–48, 52$. Waste and cultivated land. From the Old World tropics.

Danthonia

Danthonia compressa Austin—(Figure 26). $2n = 36$. Dry, open woodlands, clearings. [*D. alleni* Austin]

Danthonia spicata (Linnaeus) P. Beauvois—Poverty Oat-grass (Figure 27). $2n = 36$. Dry, sterile soil. [*D. spicata* var. *longipila* Scribner & Merrill; *D. spicata* var. *pinetorum* Piper]

Deschampsia

Deschampsia cespitosa (Linnaeus) P. Beauvois—Tufted Hairgrass (Figure 27). $2n = 18, 24–28, 49, 52, 56$. Meadows, fields, riverbanks, gravelly shores. [*D. cespitosa* var. *glauca* (Hartman) Lindman f.; *D. CESPITOSA* var. *PARVIFLORA* (Thuiller) Cosson & Germain de Saint Pierre (possibly misapplied)]

DESCHAMPSIA DANTHONIOIDES (Trinius) Munro ex Bentham—Annual Hairgrass (Figure 27). $2n = 26$. Wool waste. From farther west.

Deschampsia flexuosa (Linnaeus) Trinius—Common Hairgrass (Figure 27). $2n = 14, 26, 28, 32, 42, 56$. Dry open soil, ledges.

Desmazeria

DESMAZERIA RIGIDA (Linnaeus) Tutin—(Figure 28). $2n = 14$, 28. Waste places. From Europe. [*SCLEROPOA RIGIDA* (Linnaeus) Grisebach]

Digitaria

Digitaria cognata (Schultes) Pilger—Fall Witchgrass (Figure 28). $2n = 36$, 70, 72. Dry, sandy soil near rivers. [*Leptoloma cognatum* (Schultes) Chase]

Digitaria filiformis (Linnaeus) Koeler—Slender Crabgrass (Figure 28). $2n = 36$, 54. Dry, gravelly or sandy, open soil.

DIGITARIA ISCHAEMUM (Schreber) Muhlenberg—Smooth Crabgrass (Figure 28). $2n = 36$, 45. Rail yards, dry, sandy soil, waste ground. From Eurasia.

DIGITARIA SANGUINALIS (Linnaeus) Scopoli—Common Crabgrass (Figure 29). $2n = 18$–76. Yards, gardens, waste places, roadsides. From Europe.

DIGITARIA VIOLASCENS Link—(Figure 29). $2n = 18$, 36. Old fields. From farther south.

—*Digitaria* hybrids—

DIGITARIA ISCHAEMUM (Schreber) Muhlenberg × *D. SANGUINALIS* (Linnaeus) Scopoli—(Figure 29).

Distichlis

Distichlis spicata (Linnaeus) Greene—Seashore Saltgrass (Figure 29). $2n = 40$. Salt marshes.

Echinochloa

ECHINOCHLOA COLONA (Linnaeus) Link—Jungle-rice (Figure 30). $2n = 30$, 32, 36, 48, 52, 54, 56, 72, 96. Waste places, cultivated fields, ditches. From the Old World tropics.

ECHINOCHLOA CRUSGALLI (Linnaeus) P. Beauvois—Barnyard-grass (Figure 30). $2n = 18, 36, 48, 54, 56, 72$. Roadsides, waste places, cultivated ground. From the Old World.

ECHINOCHLOA FRUMENTACEA Link—Japanese Millet (Figure 30). $2n = 48, 54$. Waste ground, roadsides, fields. From eastern Asia. [*E. CRUSGALLI* (Linnaeus) P. Beauvois var. *FRUMENTACEA* (Link) W. F. Wight]

Echinochloa muricata (P. Beauvois) Fernald var. *muricata*—(Figure 30). $2n = 36, 48$. Marshes, shores, waste places, roadsides. [*E. pungens* (Poiret) Rydberg]

Echinochloa muricata (P. Beauvois) Fernald var. *microstachya* Wiegand—(Figure 31). $2n = 36$. Marshes, shores, waste places, roadsides. [*E. muricata* var. *occidentalis* Wiegand; *E. pungens* (Poiret) Rydberg var. *microstachya* (Wiegand) Fernald & Griscom; *E. pungens* var. *wiegandii* Fassett]

Echinochloa walteri (Pursh) Heller—(Figure 31). $2n = 36$. Shores, salt marsh borders, wet places.

Eleusine

ELEUSINE INDICA (Linnaeus) Gaertner—Wiregrass (Figure 31). $2n = 18, 36, 54$. Waste places, yards. From the Old World.

Elymus

Elymus canadensis Linnaeus—Canada Wild Rye (Figure 31). $2n = 14, 28, 42$. Dry, sandy, gravelly, or rocky soil, railroads.

Elymus glabriflorus (Vasey) Scribner & C. R. Ball—(Figure 32). $2n = 28$. Rich thickets and alluvium. [*E. virginicus* Linnaeus var. *glabriflorus* (Vasey) Bush]

Elymus hystrix Linnaeus—Bottlebrush-grass (Figure 32). $2n = 28$. Rich woods and thickets. [*Hystrix patula* Moench; *Hystrix patula* var. *bigeloviana* (Fernald) Deam]

ELYMUS PYCNANTHUS (Godron) Melderis—(Figure 32). $2n =$

42. Salt marshes, sandy shores. From Europe. [*AGROPYRON PUNGENS*—misapplied; *AGROPYRON PUNGENS* (Persoon) Roemer & Schultes var. *ACADIENSE* (F. T. Hubbard) Fernald; *AGROPYRON PYCNANTHUM* (Godron) Godron & Grenier; *ELYTRIGIA PUNGENS* (Persoon) Tutin]

ELYMUS REPENS (Linnaeus) Gould—Quackgrass (Figure 32). $2n$ = 21, 28, 42, 63. Roadsides, waste places, fields. From Eurasia. [*AGROPYRON REPENS* (Linnaeus) P. Beauvois; *AGROPYRON REPENS* var. *SUBULATUM* (Schreber) Roemer & Schultes; *ELYTRIGIA REPENS* (Linnaeus) Desvaux ex W. D. Jackson]

Elymus riparius Wiegand—(Figure 33). $2n$ = 28. Moist woods, stream banks.

Elymus submuticus (Hooker) Smyth & Smyth—(Figure 33). $2n$ = 28, 42. Rich thickets, alluvium. [*E. virginicus* Linnaeus var. *submuticus* Hooker]

Elymus trachycaulus (Link) Gould ex Shinners subsp. *trachycaulus*—Slender Wheatgrass (Figure 33). $2n$ = 28. Open soils. [*Agropyron trachycaulum* (Link) Malte ex H. F. Lewis var. *trachycaulum*; *Agropyron trachycaulum* var. *glaucum* (Pease & Moore) Malte; *Agropyron trachycaulum* var. *majus* (Vasey) Fernald; *Agropyron trachycaulum* var. *novae-angliae* (Scribner) Fernald]

Elymus villosus Muhlenberg ex Willdenow—(Figure 33). $2n$ = 28. Rich woods, thickets, shores.

Elymus virginicus Linnaeus var. *virginicus*—(Figure 34). $2n$ = 28. Shores, rich thickets. [*E. virginicus* var. *australis* (Scribner & C. R. Ball) Hitchcock; *E. virginicus* var. *intermedius* (Vasey) Bush; *E. virginicus* var. *jejunus* (Ramaley) Bush]

Elymus virginicus Linnaeus var. *halophilus* (Bicknell) Wiegand—(Figure 34). Seacoast.

Elymus wiegandii Fernald—(Figure 34). $2n$ = 28. Alluvial soil, riverbanks, rich woods.

Eragrostis

Eragrostis capillaris (Linnaeus) Nees—Lacegrass (Figure 34). 2*n* = 100. Dry, sandy or rocky soil, roadsides.

ERAGROSTIS CILIANENSIS (Allioni) Vignolo-Lutati ex Janchen—Stinkgrass (Figure 35). 2*n* = 20, 40. Wasteland, cultivated fields, railroads. From Europe. [*E. MEGASTACHYA* (Koeler) Link]

ERAGROSTIS CURVULA (Schrader) Nees—Weeping Lovegrass (Figure 35). 2*n* = 20, 40, 50, 60, 70, 80. Waste areas. From South Africa.

ERAGROSTIS DIFFUSA Buckley—2*n* = 60. Waste places, fields. From farther west. [A specimen from Calais in Washington County, Maine, collected by Arthur Gilman and identified as *E. pectinacea* has been re-identified as *E. diffusa* too late to be mapped. Some recent works such as Davidse (1994) synonymize this taxon with *E. pectinacea.*]

Eragrostis frankii C. A. Meyer—(Figure 35). 2*n* = 40, 80. Sandy riverbanks, roadsides.

Eragrostis hypnoides (Lambert) Britton, Sterns & Poggenburg—Creeping Lovegrass (Figure 35). 2*n* = 20, 40. Gravelly or sandy shores.

ERAGROSTIS INTERMEDIA Hitchcock—Plains Lovegrass (Figure 36). 2*n* = 60, 72, ca. 74, 76, 80, 100, ca. 108, 120. Dry slopes. From farther south and west.

ERAGROSTIS MEXICANA Hornemann subsp. *VIRESCENS* (J. Presl) S. D. Koch & Sánchez—(Figure 36). 2*n* = 60. Ballast. From South America. [*E. VIRESCENS* J. Presl]

ERAGROSTIS MINOR Host—(Figure 36). 2*n* = 20, 40, 44, 60, 80. Roadsides, railroads, waste places. From Europe. [*E. POOIDES* P. Beauvois ex Roemer & Schultes]

Eragrostis pectinacea (Michaux) Nees ex Steudel—(Figure 36). 2*n* = 40, 60, 80. Roadsides, railroads, waste places.

ERAGROSTIS PILOSA (Linnaeus) P. Beauvois—India Lovegrass (Figure 37). $2n = 20, 30, 40, 50, 60, 72$. Roadsides, railroads, barnyards, sandy places. From eastern Asia. [*E. MULTICAULIS* Steudel]

Eragrostis spectabilis (Pursh) Steudel—Purple Lovegrass (Figure 37). $2n = 20, 40$. Coastal sands, dry sterile soil. [*E. spectabilis* var. *sparsihirsuta* Farwell]

Eremochloa

EREMOCHLOA OPHIUROIDES (Munro) Hackel—Centipede Grass (Figure 37). $2n = 18$. From Southeast Asia.

Festuca

Festuca brachyphylla Schultes & Schultes f.—Alpine Fescue (Figure 37). $2n = 28, 42$. Rocky summits at high altitudes. [*F. ovina* Linnaeus var. *brachyphylla* (Schultes & Schultes f.) Piper ex Hitchcock]

FESTUCA FILIFORMIS Pourret—Hair Fescue (Figure 38). $2n = 14, 28$. Dry fields. From Europe. [*F. CAPILLATA* Lamarck; *F. OVINA* Linnaeus var. *CAPILLATA* (Lamarck) Alefeld]

FESTUCA HETEROMALLA Pourret—(Figure 38). $2n = 42, 56, 70$. Damp soil, cart roads, disturbed sites. From Europe. [*F. rubra* Linnaeus var. *multiflora* (Hoffmann) Ascherson & Graebner]

FESTUCA NIGRESCENS Lamarck—Chewing's Fescue (Figure 38). $2n = 28, 42$. Roadsides, ditches, dry open areas. From Europe. [*F. rubra* Linnaeus var. *commutata* Gaudin]

FESTUCA OVINA Linnaeus—Sheep Fescue (Figure 38). $2n = 14, 21, 28, 42, 70$. Dry sterile soil. From Europe.

Festuca prolifera (Piper) Fernald—(Figure 39). $2n = 49, 50, 63$, ca. 70. Summits of high mountains.

FESTUCA RUBRA Linnaeus subsp. *RUBRA*—Red Fescue (Figure 39). 2*n* = 14, 42, 44, 56. Fields, roadsides, salt marshes, open habitats. From Eurasia. [*F. RUBRA* var. *JUNCEA* (Hackel) Richter]

Festuca saximontana Rydberg—Rocky Mountain Fescue (Figure 39). 2*n* = 42, 36. Mountain crests. [*F. brachyphylla* Schultes & Schultes f. var. *rydbergii* (St.-Yves) Cronquist; *F. ovina* Linnaeus var. *saximontana* (Rydberg) Gleason]

Festuca subverticillata (Persoon) E. B. Alexeev—Nodding Fescue (Figure 39). 2*n* = 42. Rich woods. [*F. obtusa* Biehler]

FESTUCA TRACHYPHYLLA (Hackel) Krajina—Hard Fescue (Figure 40). 2*n* = 14, 28, 42. Fields. From Europe. [*F. OVINA* Linnaeus var. *DURIUSCULA*—misapplied]

Gastridium

GASTRIDIUM PHLEOIDES (Nees & Meyen) C. E. Hubbard—(Figure 40). 2*n* = 28. Wool waste, rubbish. From southwestern Asia and northeastern Africa. [Commonly identified as *G. ventricosum* (Gouan) Schinz & Thellung]

Glyceria

Glyceria acutiflora Torrey—(Figure 40). 2*n* = 20, 40. Shallow water of pools, ponds, and streams.

Glyceria borealis (Nash) Batchelder—Northern Manna-grass (Figure 40). 2*n* = 20. Shallow water, wet places.

Glyceria canadensis (Michaux) Trinius—Rattlesnake Grass (Figure 41). 2*n* = 60. Swamps, wet woods, shores.

Glyceria fluitans (Linnaeus) R. Brown—Float-grass (Figure 41). 2*n* = 20, 40. Shallow water.

Glyceria grandis S. Watson—Reed Meadow Grass (Figure 41). 2*n* = 20. Swamps, ditches, shores.

GLYCERIA MAXIMA (Hartman) Holmberg—(Figure 41). 2*n* = 56, 60. Ditches. From Eurasia. [*G. SPECTABILIS* Mertens & Koch]

Glyceria melicaria (Michaux) F. T. Hubbard—(Figure 42). 2*n* = 40. Wet woods.

Glyceria obtusa (Muhlenberg) Trinius—(Figure 42). 2*n* = 40. Wet sandy soils, swamps, wet woods.

Glyceria septentrionalis Hitchcock—Floating Manna-grass (Figure 42). 2*n* = 20, 40. Swamps, shores, meadows.

Glyceria striata (Lamarck) Hitchcock—Fowl Meadow Grass (Figure 42). 2*n* = 20. Wet places. [*G. striata* var. *stricta* (Scribner) Fernald]

—*Glyceria* hybrids—

Glyceria acutiflora Torrey × *G. septentrionalis* Hitchcock—(Figure 43). Shallow water sloughs in meadows.

Glyceria × *laxa* (Scribner) Scribner—(Figure 43). 2*n* = 42, 46. Swampy woods. [*G. canadensis* (Michaux) Trinius var. *laxa* (Scribner) Hitchcock] Parentage uncertain.

Hierochloë

Hierochloë alpina (Swartz ex Willdenow) Roemer & Schultes subsp. *orthantha* (Sørensen) G. Weim—Alpine Sweetgrass (Figure 43). 2*n* = 56–78. Siliceous rock and dry peat at high altitudes.

Hierochloë odorata (Linnaeus) P. Beauvois—Sweetgrass (Figure 43). 2*n* = 28, 42, 49, 56. Meadows, shores, salt marshes.

Holcus

HOLCUS LANATUS Linnaeus—Velvet Grass (Figure 44). 2*n* = 14, 28. Meadows, roadsides, sterile fields. From Europe.

HOLCUS MOLLIS Linnaeus—(Figure 44). 2*n* = 14, 28, 35, 42, 49. Wasteland. From Europe.

Hordeum

Hordeum jubatum Linnaeus—Squirrel-tail Grass (Figure 44). $2n = 14, 28, 42, 56$. Roadsides, railroads, salt marshes, beaches.

HORDEUM MURINUM Linnaeus subsp. *LEPORINUM* (Link) Arcangeli—(Figure 44). $2n = 14, 28, 42$. Moist waste places. From Europe. [*H. LEPORINUM* Link]

HORDEUM PUSILLUM Nuttall—Little Barley (Figure 45). $2n = 14$. Roadsides, marsh borders. From farther south.

HORDEUM VULGARE Linnaeus—Barley (Figure 45). $2n = 7, 14, 15, 28, 42$. Waste areas, roadsides. From Europe. [*H. VULGARE* var. *TRIFURCATUM* (Schlechtendal) Alefeld]

Koeleria

KOELERIA MACRANTHA (Ledebour) Schultes—Junegrass (Figure 45). $2n = 14, 15, 16, 28, 42, 56, 70, 84$. Dry soil, sands, open woods. From farther west. [*K. CRISTATA*—illegitimate name; *K. PYRAMIDATA*—misapplied]

Leersia

Leersia oryzoides (Linnaeus) Swartz—Rice Cutgrass (Figure 45). $2n = 48$. Swamps, shores, ditches.

Leersia virginica Willdenow—Whitegrass (Figure 46). $2n = 48$. Shaded riverbanks, moist woods, damp thickets. [*L. virginica* var. *ovata* (Poiret) Fernald]

Leptochloa

Leptochloa fascicularis (Lambert) A. Gray—(Figure 46). $2n = 20, 40$. Salt marshes and seacoasts. [*L. fascicularis* var. *acuminata* (Nash) Gleason; *L. fascicularis* var. *maritima* (Bicknell) Gleason; *Diplachne acuminata* Nash; *Diplachne maritima* Bicknell]

LEPTOCHLOA PANICEA (Retzius) Ohwi subsp. *MUCRONATA* (Michaux) Nowack—Red Sprangletop (Figure 46). $2n = 20$.

Gardens, fields. From farther south. [*L. FILIFORMIS* (Lambert) P. Beauvois; *L. MUCRONATA* (Michaux) Kunth]

Leymus

Leymus mollis (Trinius) Pilger—American Dunegrass (Figure 46). $2n = 28, 56$. Sea beaches. [*Elymus arenarius* Linnaeus var. *villosus* Meyer; *Elymus mollis* Trinius]

Lolium

LOLIUM ARUNDINACEUM (Schreber) Darbyshire—Reed Fescue (Figure 47). $2n = 28, 42, 56, 63, 70$. Roadsides, meadows. From Europe. [*FESTUCA ARUNDINACEA* Schreber; *FESTUCA ELATIOR* Linnaeus in part; *FESTUCA PRATENSIS*—misapplied]

LOLIUM GIGANTEUM (Linnaeus) Darbyshire—(Figure 47). $2n = 42$. Waste places. From Europe. [*FESTUCA GIGANTEA* (Linnaeus) Villars]

LOLIUM MULTIFLORUM Lambert—Italian Ryegrass (Figure 47). $2n = 14$. Fields, roadsides. From Europe. [*L. MULTIFLORUM* var. *DIMINUTUM* Mutel; *L. PERENNE* Linnaeus var. *ARISTATUM* Willdenow]

LOLIUM PERENNE Linnaeus—Ryegrass (Figure 47). $2n = 14, 28$. Fields, roadsides. From Europe.

LOLIUM PRATENSE (Hudson) Darbyshire—Meadow Fescue (Figure 48). $2n = 14, 28$. Fields, roadsides. From Europe. [*FESTUCA PRATENSIS* Hudson; *FESTUCA ELATIOR* Linnaeus in part]

LOLIUM TEMULENTUM Linnaeus—Darnel (Figure 48). $2n = 14$. Waste places. From Europe.

Lycurus

LYCURUS PHLEOIDES Kunth—Wolftail (Figure 48). $2n = 40$. Wool waste. From farther west.

Mibora

MIBORA MINIMA (Linnaeus) Desvaux—(Figure 48). $2n = 14$. Nurseries. From Europe.

Microstegium

MICROSTEGIUM VIMINEUM (Trinius) A. Camus—(Figure 49). $2n = 40$. Roadsides. From tropical Asia.

Milium

Milium effusum Linnaeus—(Figure 49). $2n = 14, 26, 28$. Rich woods.

Miscanthus

MISCANTHUS SACCHARIFLORUS (Maximowicz) Hackel—Amur Silvergrass (Figure 49). $2n = 38–95$. Roadsides, waste places. From eastern Asia.

MISCANTHUS SINENSIS Andersson—Eulalia (Figure 49). $2n = 35–57$. Roadsides, old fields. From China.

Molinia

MOLINIA CAERULEA (Linnaeus) Moench—Moorgrass (Figure 50). $2n = 18, 36, 90$. Dry fields. From Europe.

Muhlenbergia

Muhlenbergia capillaris (Lamarck) Trinius—Hairgrass (Figure 50). Dry, exposed ledges.

Muhlenbergia frondosa (Poiret) Fernald—(Figure 50). $2n = 40$. Damp, open woods, shores.

Muhlenbergia glomerata (Willdenow) Trinius—Marsh Muhly (Figure 50). $2n = 20$. Swamps, meadows, bogs. [*M. glomerata* var. *cinnoides* (Link) F. J. Hermann]

Muhlenbergia mexicana (Linnaeus) Trinius—(Figure 51). $2n = 40$. Shores, wet woods, roadsides.

MUHLENBERGIA RACEMOSA (Michaux) Britton, Sterns & Poggenburg—(Figure 51). $2n = 40$. Dry soil, railroads. From farther west.

Muhlenbergia richardsonis (Trinius) Rydberg—Mat Muhly (Figure 51). $2n = 40$. Gravelly river shores.

Muhlenbergia schreberi J. F. Gmelin—Nimble Will (Figure 51). $2n = 20, 40$. Disturbed, damp or wet places, lawns, gardens, roadsides.

Muhlenbergia sobolifera (Muhlenberg) Trinius—(Figure 52). $2n = 40$. Dry woods (often rocky and calcareous).

Muhlenbergia sylvatica Torrey—(Figure 52). $2n = 40$. Gravelly shores, rich woods. [*M. sylvatica* var. *robusta* Fernald]

Muhlenbergia tenuiflora (Willdenow) Britton, Sterns & Poggenburg—(Figure 52). $2n = 40$. Rocky woods, shaded cliffs.

Muhlenbergia uniflora (Muhlenberg) Fernald—(Figure 52). $2n =$ ca. 42. Bogs, meadows, sandy shores, roadsides.

Nardus

NARDUS STRICTA Linnaeus—Moor Matgrass (Figure 53). $2n = 16, 26, 27$, ca. 28, 30. Old fields, grassy riverbanks. From Europe.

Oryzopsis

Oryzopsis asperifolia Michaux—(Figure 53). $2n = 46, 48$. Dry woods.

Oryzopsis canadensis (Poiret) Torrey—(Figure 53). $2n = 22$. Dry, sandy or rocky woods.

Oryzopsis pungens (Torrey ex Sprengel) Hitchcock—(Figure 53). $2n = 22, 24$. Dry, sandy or rocky woods.

Panicum

Panicum acuminatum Swartz var. *acuminatum*—(Figure 54). $2n = 18$. Dry sand or beaches. [*P. auburne* Ashe; *P. lanuginosum* Elliott]

Panicum acuminatum Swartz var. *fasciculatum* (Torrey) A. A. Beetle—(Figure 54). $2n = 18$. Thin, dry woodlands, dry or moist sterile soil in the open. [*P. huachucae* Ashe var. *fasciculatum* (Torrey) F. T. Hubbard; *P. implicatum* Scribner; *P. lanuginosum* Elliott var. *fasciculatum* (Torrey) Fernald; *P. lanuginosum* var. *implicatum* (Scribner) Fernald; *P. lanuginosum* var. *tennesseense* (Ashe) Gleason; *P. subvillosum* Ashe; *P. tennesseense* Ashe]

Panicum acuminatum Swartz var. *lindheimeri* (Nash) A. A. Beetle—(Figure 54). $2n = 18$. Thin, dry woodlands, dry or moist sterile soil in the open. [*P. lanuginosum* Elliott var. *lindheimeri* (Nash) Fernald; *P. lanuginosum* var. *septentrionale* Fernald; *P. lindheimeri* Nash]

Panicum amarum Elliott var. *amarum*—(Figure 54). $2n = 54$. Sandy coasts.

Panicum amarum var. *amarulum* (Hitchcock & Chase) P. Palmer—(Figure 55). $2n = 36$. Sea beaches. [*P. amarulum* Hitchcock & Chase]

Panicum boreale Nash–(Figure 55). $2n = 18$. Shores, meadows, moist woods, fields. [*P. bicknellii* Nash var. *bicknellii; P. bicknellii* var. *calliphyllum* (Ashe) Gleason; *P. calliphyllum* Ashe]

Panicum boscii Poiret—(Figure 55). $2n = 18, 36$. Dry woods. [*P. boscii* var. *molle* (Vasey) Hitchcock & Chase]

Panicum capillare Linnaeus—Witchgrass (Figure 55). $2n = 18$. Open sandy or stony soil, roadsides, waste places, cultivated land. [*P. capillare* var. *agreste* Gattinger; *P. capillare* var. *occidentale* Rydberg]

Panicum clandestinum Linnaeus—(Figure 56). 2*n* = 36. Thickets, shores, alluvial woods borders.

Panicum columbianum Scribner—(Figure 56). 2*n* = 18. Sandy open ground, thin woods. [*P. columbianum* var. *oricola* (Hitchcock & Chase) Fernald; *P. columbianum* var. *thinium* Hitchcock & Chase; *P. tsugetorum* Nash]

Panicum commutatum Schultes var. *commutatum.* 2*n* = 18. Open woods, open sandy or rocky places. [*P. divergens* Kunth] This taxon is not mapped since we did not distinguish between the varieties of *P. commutatum* when we recorded specimen data.

Panicum commutatum Schultes var. *ashei* (G. Pearson ex Ashe) Fernald—(Figure 56). 2*n* = 18. Dry, open woods, openings. [*P. ashei* G. Pearson ex Ashe]

Panicum depauperatum Muhlenberg—(Figure 56). 2*n* = 18. Dry or sandy soil, open woods. [*P. depauperatum* var. *involutum* (Torrey) Wood; *P. depauperatum* var. *psilophyllum* Fernald]

Panicum dichotomiflorum Michaux var. *dichotomiflorum*—Fall Panicum (Figure 57). 2*n* = 36, 54. Moist soil, shores, roadsides, railroads, waste areas. [*P. dichotomiflorum* var. *geniculatum* (Wood) Fernald]

Panicum dichotomiflorum Michaux var. *puritanorum* Svenson—(Figure 57). Damp sands, pond margins.

Panicum dichotomum Linnaeus var. *dichotomum*—(Figure 57). 2*n* = 18. Dry, open woods. [*P. dichotomum* var. *barbulatum* (Michaux) Wood; *P. barbulatum* Michaux]

Panicum dichotomum Linnaeus var. *lucidum* (Ashe) Lelong—(Figure 57). 2*n* = 18. Rocky woods. [*P. lucidum* Ashe]

Panicum dichotomum Linnaeus var. *mattamuskeetense* (Ashe) Lelong—(Figure 58). 2*n* = 18. [*P. annulum* Ashe; *P. annulum* Ashe var. *glabrescens* Gleason; *P. clutei* Nash; *P. matta-*

muskeetense Ashe; *P. mattamuskeetense* Ashe var. *clutei* (Nash) Fernald]

Panicum flexile (Gattinger) Scribner—(Figure 58). 2*n* = 18. Shores in calcareous areas.

Panicum gattingeri Nash—(Figure 58). 2*n* = 18. Sandy areas, roadsides, fields, wood borders. [*P. capillare* Linnaeus var. *campestre* Gattinger]

Panicum latifolium Linnaeus—(Figure 58). 2*n* = 18. Open, usually dry, woods.

Panicum linearifolium Scribner—(Figure 59). 2*n* = 18. Dry soil, open woods, slopes. [*P. linearifolium* var. *werneri* (Scribner) Fernald; *P. werneri* Scribner]

Panicum meridionale Ashe—(Figure 59). 2*n* = 18. Dry, open habitats. [*P. meridionale* var. *albemarlense* (Ashe) Fernald; *P. albemarlense* Ashe]

Panicum microcarpon Muhlenberg ex Elliott—(Figure 59). 2*n* = 18. Woodlands, openings. [*P. nitidum* Lamarck var. *ramulosum* Torrey]

PANICUM MILIACEUM Linnaeus—Broom-corn Millet (Figure 59). 2*n* = 36, 54, 72. Roadsides, waste places. From the Old World.

Panicum oligosanthes Schultes var. *oligosanthes*—(Figure 60). 2*n* = 18. Dry, open soil.

Panicum oligosanthes Schultes var. *scribnerianum* (Nash) Fernald—(Figure 60). 2*n* = 18. Dry, open soil. [*P. scribnerianum* Nash]

Panicum ovale Elliott var. *pseudopubescens* (Nash) Lelong—(Figure 60). 2*n* = 18. Dry, sandy woods. [*P. addisonii* Nash; *P. commonsianum* Ashe var. *commonsianum; P. commonsianum* var. *addisonii* (Nash) Fernald; *P. pseudopubescens*

Nash; *P. villosissimum* Nash var. *pseudopubescens* (Nash) Fernald]

Panicum philadelphicum Bernhardi ex Trinius—(Figure 60). $2n = 18$. Shores, woods, roadsides. [*P. tuckermanii* Fernald]

Panicum polyanthes Schultes—(Figure 61). $2n = 18$. Dry woods. [The identity of all New England voucher specimens is open to question.]

Panicum rigidulum Bose ex Nees var. *rigidulum*—(Figure 61). $2n = 18$. Shores, meadows. [*P. rigidulum* var. *condensum* (Nash) F. Seymour; *P. agrostoides* Sprengel var. *agrostoides; P. agrostoides* var. *condensum* (Nash) Fernald; *P. condensum* Nash]

Panicum rigidulum Bose ex Nees var. *elongatum* (Pursh) Lelong—(Figure 61). $2n = 18$. Swamps, shores, meadows. [*P. stipitatum* Nash]

Panicum rigidulum Bosc ex Nees var. *pubescens* (Vasey) Lelong—(Figure 61). $2n = 18$. Shores, meadows, bogs. [*P. longifolium* Torrey]

Panicum scabriusculum Elliott—(Figure 62). $2n = 18$. Moist open ground. [*P. aculeatum* Hitchcock & Chase; *P. recognitum* Fernald]

Panicum scoparium Lamarck—Velvet Panic-grass (Figure 62). $2n = 18$. Damp soil.

Panicum sphaerocarpon Elliott—(Figure 62). $2n = 18$. Dry fields and woods, beaches.

Panicum spretum Schultes—(Figure 62). $2n = 18$. Shores, meadows.

Panicum verrucosum Muhlenberg—(Figure 63). $2n = 36$. Moist soil, shores.

Panicum villosissimum Nash—(Figure 63). $2n = 18$. Open woods.

Panicum virgatum Linnaeus—Switchgrass (Figure 63). 2*n* = 18–154. Dry soil, sandy or gravelly shores, fields. [*P. virgatum* var. *cubense* Grisebach; *P. virgatum* var. *spissum* Linder]

Panicum wrightianum Scribner—(Figure 63). 2*n* = 18. Pond shores.

Panicum xanthophysum A. Gray—(Figure 64). 2*n* = 36. Sandy, open woods and clearings.

—*Panicum* hybrids—

Panicum dichotomum Linnaeus × *P. latifolium* Linnaeus—(Figure 64).

Panicum × *scoparioides* (Ashe) Mohlenbrock—(Figure 64). 2*n* = 18. Open woods. [*P. acuminatum* Swartz × *P. oligosanthes* Schultes; *P. villosissimum* Nash var. *scoparioides* (Ashe) Fernald]

Pappophorum

PAPPOPHORUM VAGINATUM Buckley—(Figure 64). 2*n* = 60. Wool waste. From farther south and west. [*P. MUCRONULATUM*—misapplied]

Pascopyrum

PASCOPYRUM SMITHII (Rydberg) Á. Löve—Western Wheatgrass (Figure 65). 2*n* = 56. Railroads. From farther west. [*AGROPYRON SMITHII* Rydberg; *ELYTRIGIA SMITHII* (Rydberg) Nevski]

Paspalum

Paspalum laeve Michaux—(Figure 65). 2*n* = 40, 58, 80. Meadows, shores, damp sandy fields. [*P. laeve* var. *circulare* (Nash) Fernald; *P. laeve* var. *pilosum* Scribner; *P. circulare* Nash; *P. longipilum* Nash]

Paspalum setaceum Michaux var. *setaceum*—(Figure 65). 2*n* = 20, 40, 50. Sandy fields.

Paspalum setaceum Michaux var. *muhlenbergii* (Nash) D. J. Banks—(Figure 65). 2*n* = 20, 40, 50. Dry fields, pastures. [*P. ciliatifolium* Michaux var. *muhlenbergii* (Nash) Fernald; *P. pubescens* Muhlenberg]

Paspalum setaceum Michaux var. *psammophilum* (Nash) D. J. Banks—(Figure 66). 2*n* = 20, 40, 50. Dry, sandy fields near the coast. [*P. psammophilum* Nash]

Phalaris

Phalaris arundinacea Linnaeus—Reed Canary-grass (Figure 66). 2*n* = 14, 28, 35, 42, 48. Shores, wet meadows.

PHALARIS CANARIENSIS Linnaeus—Canary-grass (Figure 66). 2*n* = 12. Roadsides, railroads, waste places. From Europe.

Phleum

Phleum alpinum Linnaeus—Mountain Timothy (Figure 66). 2*n* = 14, 28. High altitudes.

PHLEUM ARENARIUM Linnaeus—(Figure 67). 2*n* = 14. Waste areas, ballast. From Europe and North Africa.

PHLEUM PRATENSE Linnaeus—Timothy (Figure 67). 2*n* = 14, 21, 28–84. Fields, roadsides. From Eurasia. [*P. PRATENSE* var. *NODOSUM* (Linnaeus) Hudson]

PHLEUM SUBULATUM (Savi) Ascherson & Graebner—(Figure 67). 2*n* = 14. Waste areas, ballast. From the Mediterranean.

Phragmites

Phragmites australis (Cavanilles) Trinius ex Steudel—Common Reed (Figure 67). 2*n* = 36, 40, 42–59, 72, 84, 96. Marshes, shores, ditches. [*P. communis* Trinius var. *communis; P. communis* var. *berlandieri* (Fournier) Fernald]

Phyllostachys

PHYLLOSTACHYS DULCIS McClure—Sweetshoot Bamboo (Figure 68). Barnyards. From China.

Piptatherum

Piptatherum racemosum (Smith) Eaton—Black Mountain-rice (Figure 68). $2n = 46, 48$. Dry, often calcareous, rocky woods. [*Oryzopsis racemosa* (Smith) Ricker]

Piptochaetium

Piptochaetium avenaceum (Linnaeus) Parodi—Black Oat-grass (Figure 68). $2n = 22, 28$. Dry openings, open woods. [*Stipa avenacea* Linnaeus]

Poa

Poa alsodes A. Gray—(Figure 68). Alluvial woods.

POA ANNUA Linnaeus—Annual Bluegrass (Figure 69). $2n = 14$, 24–26, 28, 52. Roadsides, cultivated fields, waste places. From Eurasia.

POA BULBOSA Linnaeus—Bulbous Bluegrass (Figure 69). $2n = 14$, 21, 24, 28, 31–58. Lawns, dry fields. From Eurasia.

POA CHAPMANIANA Scribner—(Figure 69). Cultivated fields, weedy places. From farther south and west.

POA COMPRESSA. Linnaeus—Canada Bluegrass (Figure 69). $2n = 14–56$. Dry soil, roadsides, waste places. From Eurasia.

Poa glauca Vahl—(Figure 70). $2n = 42–78$. Alpine meadows and ravines.

Poa laxa Haenke subsp. *fernaldiana* (Nannfeldt) N. Hylander—(Figure 70). $2n = 42$. Alpine meadows. [*P. fernaldiana* Nannfeldt]

POA NEMORALIS Linnaeus subsp. *NEMORALIS*—Wood Bluegrass (Figure 70). $2n = 14$, 28–70. Dry woods, roadsides. From Europe.

Poa palustris Linnaeus—Fowl Meadow-grass (Figure 70). 2*n* = 28, 30, 32, 42. Moist woods, shores, swamps, meadows.

POA PRATENSIS Linnaeus subsp. *PRATENSIS*—Kentucky Bluegrass (Figure 71). 2*n* = 14, 21, 25–124. Roadsides, fields, meadows. From Europe.

Poa pratensis Linnaeus subsp. *alpigena* (Fries ex Blytt) Hiitonen—(Figure 71). 2*n* = 28–127. Alpine regions. [*P. alpigena* (Fries ex Blytt) Lindman f.; *P. arctica*—misapplied]

POA PRATENSIS Linnaeus subsp. *ANGUSTIFOLIA* (Linnaeus) Arcangeli. 2*n* = 46–72. Dry soil in the open. From Europe. [*P. ANGUSTIFOLIA* Linnaeus] This taxon is not mapped since we did not distinguish between the subspecies *PRATENSIS* and *ANGUSTIFOLIA* of *P. PRATENSIS* when we recorded specimen data.

Poa saltuensis Fernald & Wiegand—(Figure 71). 2*n* = 28. Rich, usually dry, woods. [*P. saltuensis* var. *microlepis* Fernald; *P. languida* Hitchcock]

POA TRIVIALIS Linnaeus—Rough Bluegrass (Figure 71). 2*n* = 14, 28, 72. Springheads, brook sides, glades. From Eurasia.

Polypogon

POLYPOGON MONSPELIENSIS (Linnaeus) Desfontaines—Rabbitfoot Grass (Figure 72). 2*n* = 14, 26, 28, 35, 42. Wool waste, waste places. From Europe.

Puccinellia

PUCCINELLIA DISTANS (Linnaeus) Parlatore subsp. *DISTANS*—(Figure 72). 2*n* = 14, 28, 42. Roadsides, waste places. From Europe.

PUCCINELLIA DISTANS (Linnaeus) Parlatore subsp. *BOREALIS* (Holmberg) W. E. Hughes—(Figure 72). 2*n* = 42. Roadsides, waste places. From Europe. [*P. DISTANS* var. *ANGUSTIFOLIA* (Blytt) Holmberg]

Puccinellia fasciculata (Torrey) Bicknell—(Figure 72). $2n = 14$, 28, 42. Salt marshes, brackish shores, sandy seashores.

Puccinellia laurentiana Fernald & Weatherby—(Figure 73). $2n = 56$. Gravelly seashores.

Puccinellia maritima (Hudson) Parlatore—(Figure 73). $2n = 14$–77. Salt marshes, brackish shores.

PUCCINELLIA NUTTALLIANA (Schultes) Hitchcock—(Figure 73). $2n = 28$, 42, 56. Moist, alkaline soil. From farther west. [*P. AIROIDES* (Nuttall) S. Watson & Coulter]

Puccinellia tenella (Lange) Holmberg subsp. *alaskana* (Scribner & Merrill) Tzvelev—(Figure 73). $2n = 42$, 56. Salt marshes, gravelly beaches. [*P. paupercula* (Holmberg) Fernald & Weatherby var. *alaskana* (Scribner & Merrill) Fernald & Weatherby; *P. pumila* (Vasey) Hitchcock]

Schizachne

Schizachne purpurascens (Torrey) Swallen—False Melic (Figure 74). $2n = 20$. Rich woods.

Schizachyrium

Schizachyrium littorale (Nash) Bicknell—(Figure 74). $2n = 40$. Upper borders of sea beaches, dunes. [*Andropogon littoralis* Nash; *Andropogon scoparius* Michaux var. *littoralis* (Nash) Hitchcock; *S. scoparium* (Michaux) Nash var. *littorale* (Nash) Gould]

Schizachyrium scoparium (Michaux) Nash—Little Bluestem (Figure 74). $2n = 40$. Dry soil, old fields, open woods. [*Andropogon scoparius* Michaux var. *scoparius; Andropogon scoparius* var. *ducis* Fernald & Griscom; *Andropogon scoparius* var. *frequens* F. T. Hubbard; *Andropogon scoparius* var. *neomexicanus* (Nash) Hitchcock; *Andropogon scoparius* var. *septentrionalis* Fernald & Griscom]

Secale

SECALE CEREALE Linnaeus—Rye (Figure 74). $2n = 7, 14, 16, 27–29$. Waste places, roadsides. From Eurasia.

Setaria

SETARIA FABERI R. A. W. Herrmann—(Figure 75). $2n = 36$. Roadsides, railroads, waste places, fields. From eastern Asia.

SETARIA ITALICA (Linnaeus) P. Beauvois—Foxtail Millet (Figure 75). $2n = 18$. Cultivated land, waste places, roadsides. From the Old World.

Setaria parviflora (Poiret) Kerguélen—(Figure 75). $2n = 22, 36, 72$. Salt marsh borders, hillsides, waste places. [*S. geniculata*—misapplied]

SETARIA PUMILA (Poiret) Roemer & Schultes—Yellow Foxtail (Figure 75). $2n = 35, 36, 44, 72$. Dry sandy soil, roadsides, cultivated land, waste places. From Europe. [*S. GLAUCA*—misapplied; *S. LUTESCENS* (Weigel) F. T. Hubbard]

SETARIA VERTICILLATA (Linnaeus) P. Beauvois—Bur Foxtail (Figure 76). $2n = 18, 36, 54, 72, 108$. Waste places. From Eurasia.

SETARIA VIRIDIS (Linnaeus) P. Beauvois—Green Foxtail (Figure 76). $2n = 18, 36$. Cultivated fields, roadsides, railroads, waste places. From Europe. [*S. VIRIDIS* var. *BREVISETA* (Döll) Hitchcock; *S. VIRIDIS* var. *WEINMANNII* (Roemer & Schultes) Brand]

Sorghastrum

Sorghastrum nutans (Linnaeus) Nash—Indian Grass (Figure 76). $2n = 20, 40, 80$. Dry fields, roadsides, rocky shores of rivers.

Sorghum

SORGHUM BICOLOR (Linnaeus) Moench—Sorghum (Figure 76). $2n = 10, 20$. Waste places. From Africa. [*S. VULGARE* Persoon]

SORGHUM HALEPENSE (Linnaeus) Persoon—Johnson Grass (Figure 77). $2n$ = 18, 20, 26, 40, 60. Waste places. From the Mediterranean.

Spartina

Spartina alterniflora Loiseleur—Smooth Cordgrass (Figure 77). $2n$ = 40, 42, 56, 60, 62, 70. Salt marshes, tidal shores. [*S. alterniflora* var. *pilosa* (Merrill) Fernald]

Spartina cynosuroides (Linnaeus) Roth—Big Cordgrass (Figure 77). $2n$ = 28, 40, 42, ca. 80. Salt marshes. [*S. cynosuroides* var. *polystachya* (Michaux) Beal ex Fernald]

Spartina patens (Aiton) Muhlenberg—Saltmeadow Cordgrass (Figure 77). $2n$ = 28, 40, 42, 56. Salt marshes. [*S. patens* var. *monogyna* (M. A. Curtis) Fernald]

Spartina pectinata Link—Prairie Cordgrass (Figure 78). $2n$ = 28, 40, 42, 84. Shores, meadows, lowlands. [*S. pectinata* var. suttiei (Farwell) Fernald]

—*Spartina* hybrids—

Spartina × *caespitosa* A. A. Eaton—(Figure 78). $2n$ = 40. Salt marsh borders, beaches. [*S. patens* (Aiton) Muhlenberg × *S. pectinata* Link; *S. patens* var. *caespitosa* (A. A. Eaton) Hitchcock]

Sphenopholis

Sphenopholis intermedia Rydberg—(Figure 78). $2n$ = 14. Meadows, shores, damp slopes. [*S. obtusata* (Michaux) Scribner var. *major* (Torrey) K. S. Erdman]

Sphenopholis nitida (Biehler) Scribner—(Figure 78). $2n$ = 14. Rich, rocky woods.

Sphenopholis obtusata (Michaux) Scribner—Prairie Wedgegrass (Figure 79). $2n$ = 14. Wood borders, shores, dry ledges. [*S.*

obtusata var. *lobata* (Trinius) Scribner; *S. obtusata* var. *pubescens* (Scribner & Merrill) Scribner]

Sphenopholis pensylvanica (Linnaeus) Hitchcock—Swamp Oats (Figure 79). 2*n* = 14. Meadows. [*Trisetum pensylvanicum* (Linnaeus) P. Beauvois ex Roemer & Schultes]

Sporobolus

Sporobolus asper (P. Beauvois) Kunth—(Figure 79). 2*n* = 54, 88, 108. Dry, sandy, open soil.

Sporobolus clandestinus (Biehler) Hitchcock—(Figure 79). 2*n* = 46, 48, 52, 54, 56. Dry, sandy or rocky soil.

SPOROBOLUS CONTRACTUS Hitchcock—Spike Dropseed (Figure 80). 2*n* = 36. Sandy soil. [*S. CRYPTANDRUS* (Torrey) A. Gray var. *STRICTUS* Scribner]

Sporobolus cryptandrus (Torrey) A. Gray—Sand Dropseed (Figure 80). 2*n* = 18, 36, 38, 72. Sandy soil, usually near seashores.

Sporobolus heterolepis A. Gray—Prairie Dropseed (Figure 80). 2*n* = 72. Dry trap (limestone or serpentine).

Sporobolus neglectus Nash—(Figure 80). 2*n* = 36. Dry open soil.

Sporobolus vaginiflorus (Torrey ex A. Gray) Wood—Poverty Grass (Figure 81). 2*n* = 54. Roadsides, sandy fields, dry, open, sterile soil. [*S. vaginiflorus* var. *inaequalis* Fernald]

Taeniatherum

TAENIATHERUM CAPUT-MEDUSAE (Linnaeus) Nevski—(Figure 81). 2*n* = 14. Waste places. From Europe. *ELYMUS CAPUT-MEDUSAE* Linnaeus]

Torreyochloa

Torreyochloa pallida (Torrey) Church var. *pallida*—(Figure 81). $2n$ = 14. Pools, pond margins. [*Glyceria pallida* (Torrey) Trinius; *Puccinellia pallida* (Torrey) R. T. Clausen]

Torreyochloa pallida (Torrey) Church var. *fernaldii* (Hitchcock) Dore ex Koyama & Kawano—(Figure 81). $2n$ = 14. Shallow water, wet places. [*Glyceria fernaldii* (Hitchcock) St. John; *Glyceria pallida* (Torrey) Trinius var. *fernaldii* Hitchcock]

Tragus

TRAGUS BERTERONIANUS Schultes—(Figure 82). $2n$ = 20. Ballast, wool waste. From the Old World.

TRAGUS RACEMOSUS (Linnaeus) Allioni—(Figure 82). $2n$ = 40. Ballast, waste areas. From the Old World.

Tridens

Tridens flavus (Linnaeus) Hitchcock—Purpletop (Figure 82). $2n$ = 40. Dry fields, roadsides. [*Triodia flava* (Linnaeus) Smyth]

Triplasis

Triplasis purpurea (Walter) Chapman—Purple Sandgrass (Figure 82). $2n$ = 40. Sand dunes.

Tripsacum

Tripsacum dactyloides (Linnaeus) Linnaeus—Eastern Gamagrass (Figure 83). $2n$ = 18, 36, 45, 54, 72, 90, 108. Shores, salt marsh borders.

Trisetum

TRISETUM FLAVESCENS (Linnaeus) P. Beauvois—Yellow Oats (Figure 83). $2n$ = 24, 28, 36, 38, 40, 42. Fields, roadsides. From Europe.

Trisetum melicoides (Michaux) Vasey ex Scribner—Purple False

Oats (Figure 83). Gravelly shores, river thickets. [*T. melicoides* var. *majus* (A. Gray) Hitchcock]

Trisetum spicatum (Linnaeus) Richter—(Figure 83). $2n = 14, 28, 42$. Wet ledges, shores. [*T. spicatum* var. *molle* (Michaux) Beal; *T. spicatum* var. *pilosiglume* Fernald]

Triticum

TRITICUM AESTIVUM Linnaeus—Wheat (Figure 84). $2n = 14, 21, 34, 41, 42, 44$. Waste places. From Eurasia.

Urochloa

UROCHLOA TEXANA (Buckley) R. D. Webster—Texas Millet (Figure 84). $2n = 36, 54$. Fields, waste places. From farther west [*PANICUM TEXANUM* Buckley]

Vahlodea

Vahlodea atropurpurea (Wahlenberg) Fries ex Hartman—Mountain Hairgrass (Figure 84). $2n = 14$. High altitudes. [*Deschampsia atropurpurea* (Wahlenberg) Scheele]

Vulpia

VULPIA BROMOIDES (Linnaeus) S. F. Gray—(Figure 84). $2n = 14$. Waste places. From Europe. [*FESTUCA DERTONENSIS* (Allioni) Ascherson & Graebner; *V. DERTONENSIS* (Allioni) Gola]

VULPIA MYUROS (Linnaeus) K. C. Gmelin—Rat-tail Fescue (Figure 85). $2n = 14, 28, 42$. Dry fields, waste places. From Europe. [*FESTUCA MEGALURA* Nuttall; *FESTUCA MYUROS* Linnaeus]

Vulpia octoflora (Walter) Rydberg var. *octoflora*—Six-weeks Fescue (Figure 85). $2n = 14$. Marsh borders, sandy waste ground.

Vulpia octoflora (Walter) Rydberg var. *glauca* (Nuttall) Fernald—

(Figure 85). $2n = 14$. Dry ledges, sandy soil. [*V. octoflora* var. *tenella* (Willdenow) Fernald; *Festuca octoflora* Walter var. *glauca* (Nuttall) Fernald; *Festuca octoflora* var. *tenella* (Willdenow) Fernald]

Zea

ZEA MAYS Linnaeus—Corn (Figure 85). $2n = 20, 21, 22$. Waste places, roadsides, margins of cultivated fields. From Mexico.

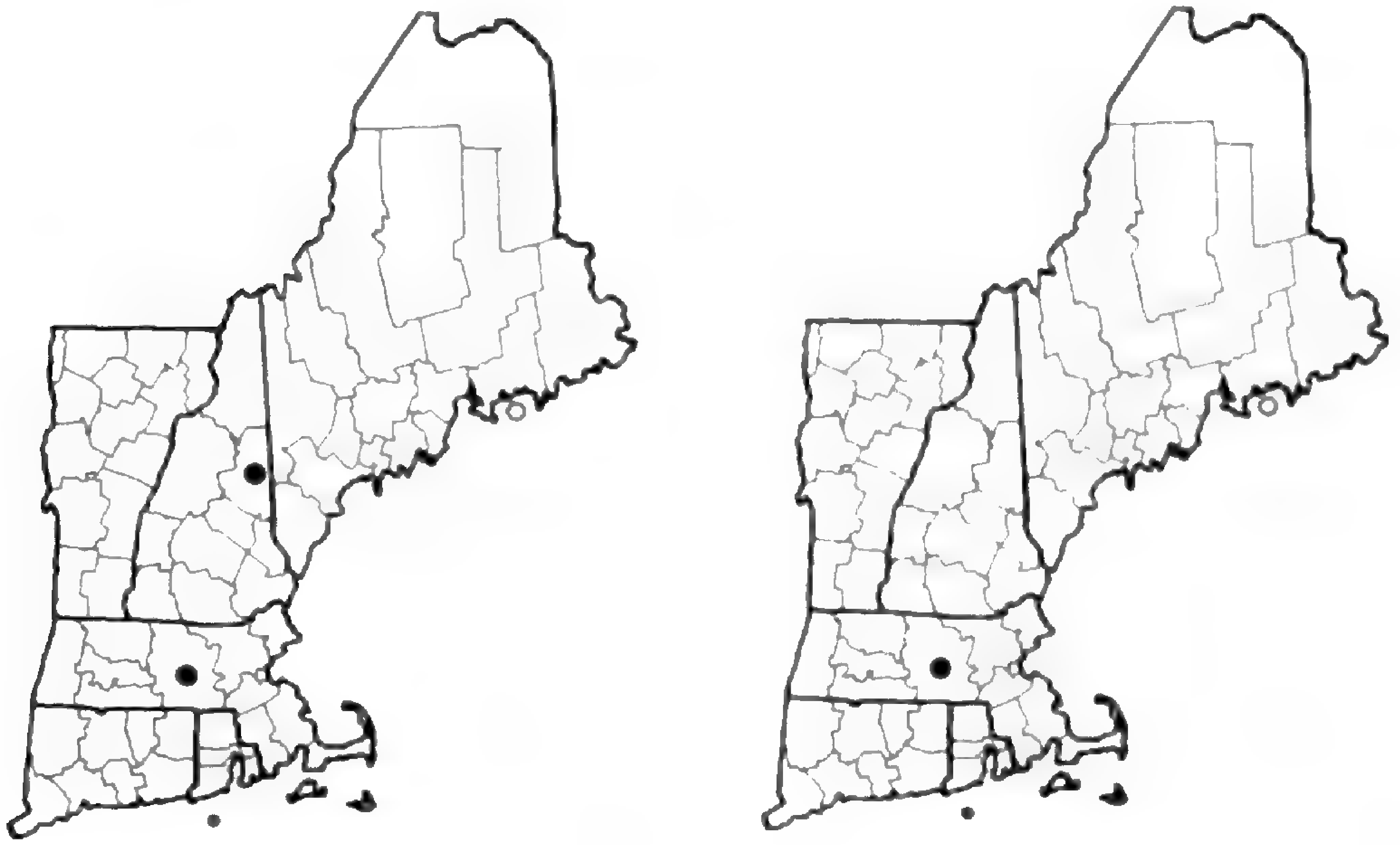
Zizania

Zizania aquatica Linnaeus—Annual Wild Rice (Figure 86). $2n = 30$. Mud flats along rivers, often tidal.

Zizania palustris Linnaeus—(Figure 86). Shallow, quiet waters. [*Z. aquatica* Linnaeus var. *angustifolia* Hitchcock]

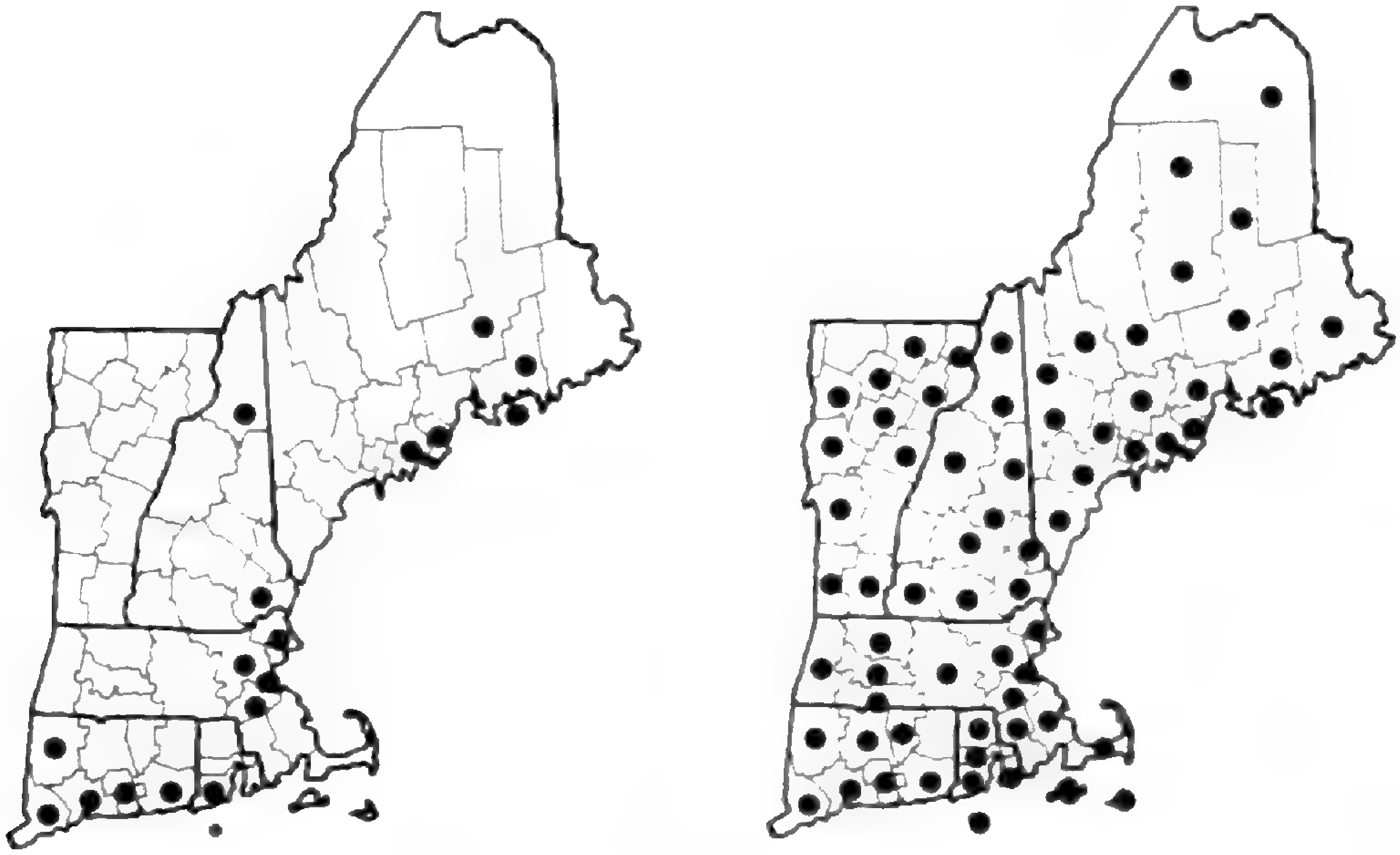
ACKNOWLEDGMENTS. We thank the curators and directors of the herbaria of Harvard University, the University of Maine, University of Massachusetts, and the University of Vermont for allowing us access to their collections. We particularly appreciate the kindness of David Barrington, Chris Campbell, and Karen Searcy for allowing use of the collections in their care outside of normal hours of operation. We are grateful also to Karen Searcy for allowing access to the notebooks of Harry E. Ahles at the University of Massachusetts and for checking some voucher specimens there. We also appreciate the check for voucher specimens by Steve Rawson, Cathy Paris, Janet Sullivan, Tom Vining, and Chris Campbell. Mary Barkworth graciously reviewed the manuscript and very generously provided updates for the nomenclature and taxonomy of several groups to bring them into agreement with the forthcoming *Manual of Grasses for the Continental United States and Canada*. Craig Greene provided additional useful information relating to *Calamagrostis*. Kancheepuram N. Gandhi generously gave assistance on some nomenclatural issues, but any errors in this work are the responsibility of the authors.

Figure 1. Key map for counties of the New England states (and Mt. Desert Island, Maine; Block Island, Rhode Island; arbitrary divisions of larger Maine counties and of Coös County, New Hampshire).



AGROPYRON CRISTATUM

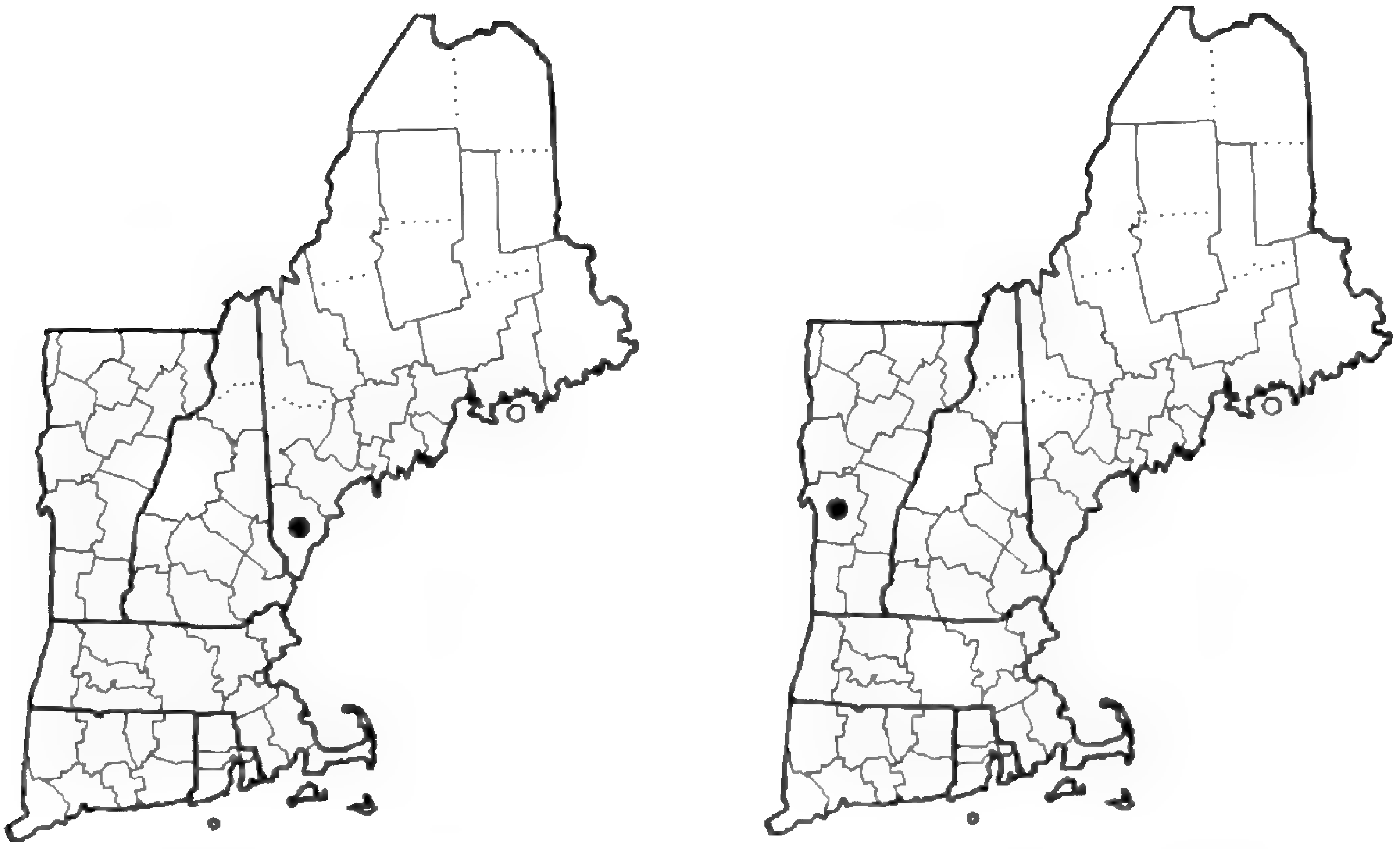
AGROPYRON DESERTORUM



AGROSTIS CANINA

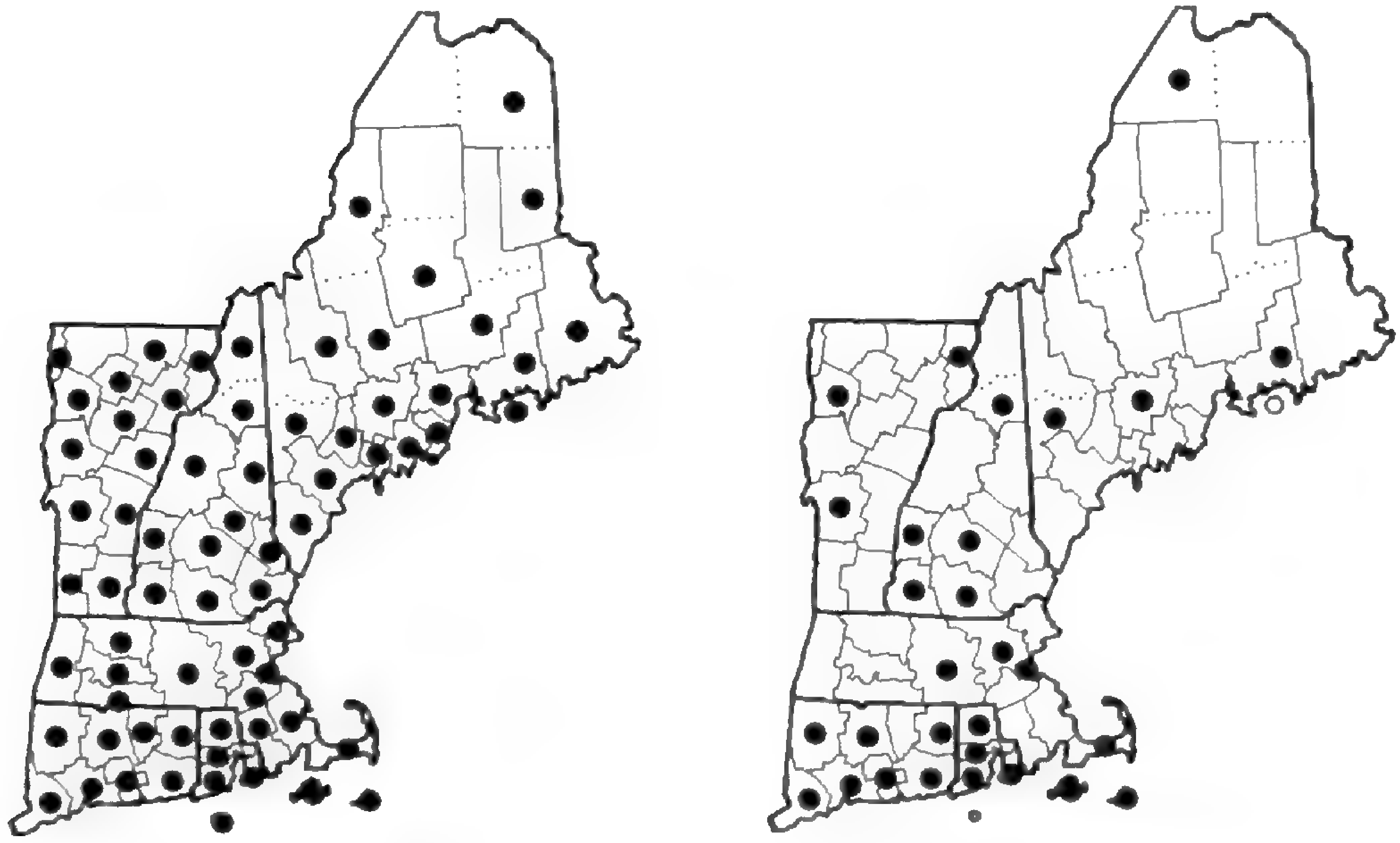
AGROSTIS CAPILLARIS

Figure 2. Distribution maps for *AGROPYRON CRISTATUM*, *A. DESERTORUM*, *AGROSTIS CANINA* and *A. CAPILLARIS*.



AGROSTIS ELLIOTTIANA

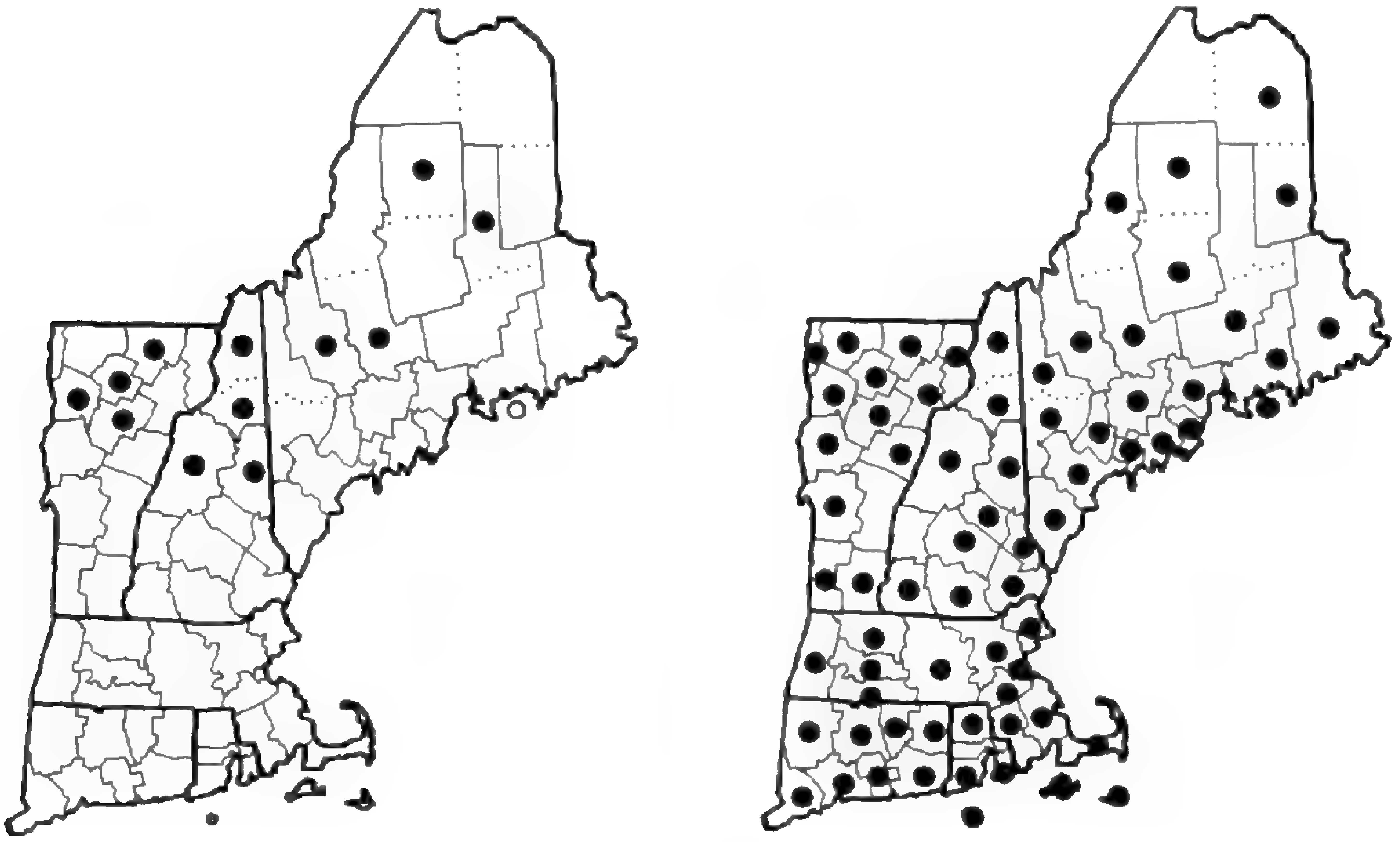
AGROSTIS EXARATA



AGROSTIS GIGANTEA

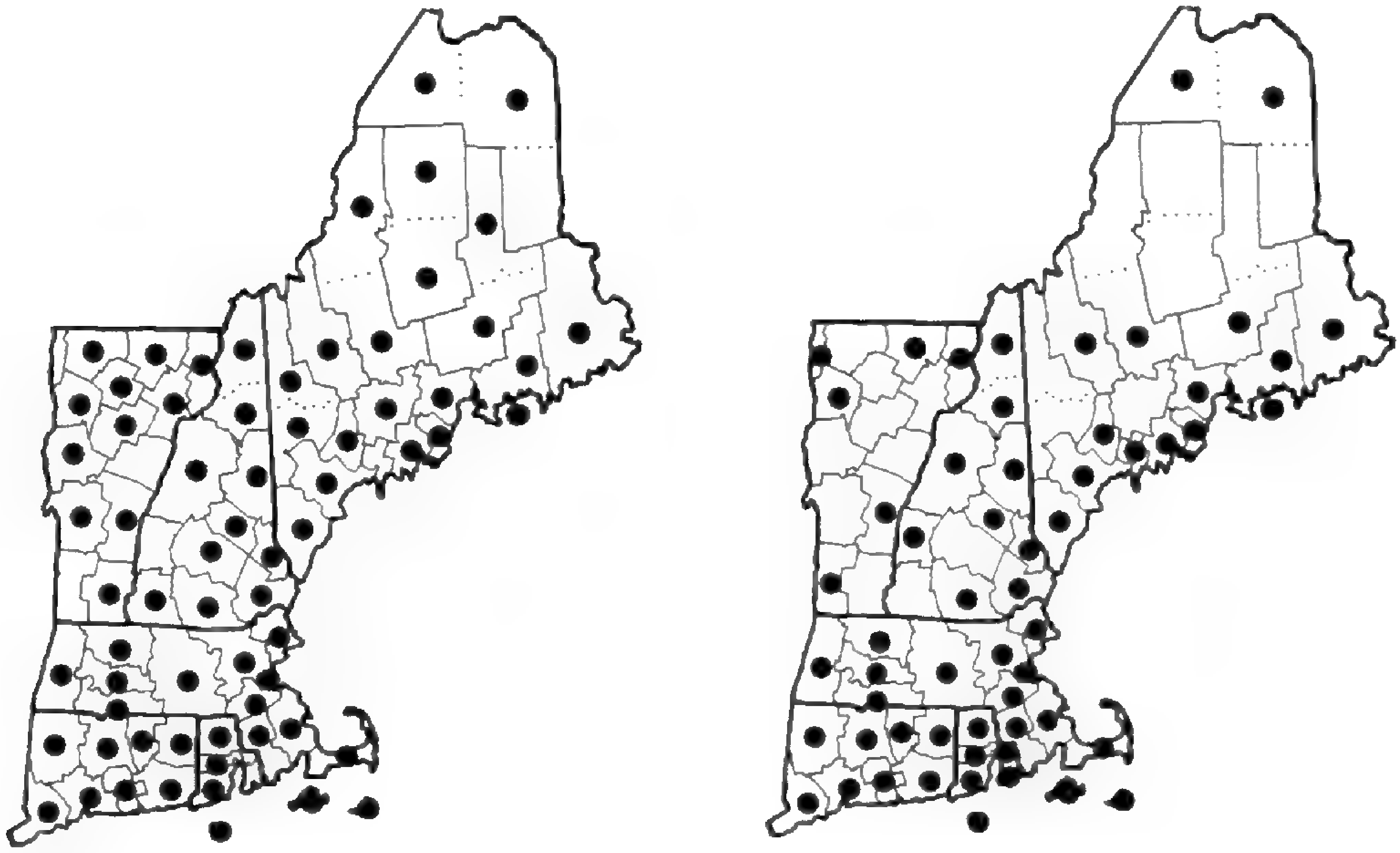
Agrostis hyemalis

Figure 3. Distribution maps for *AGROSTIS ELLIOTTIANA*, *A. EXARATA*, *A. GIGANTEA* and *A. hyemalis*.



Agrostis mertensii

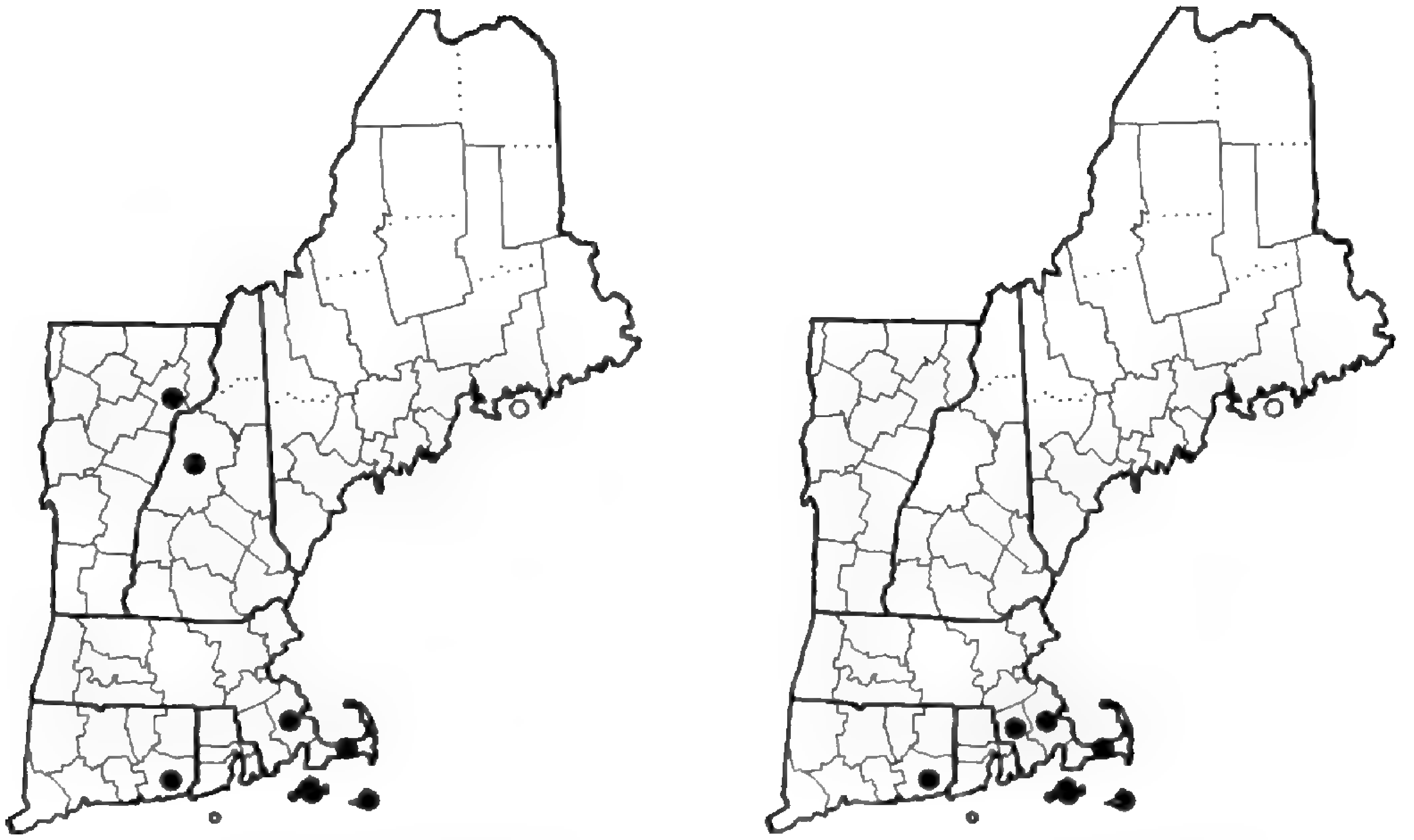
Agrostis perennans



Agrostis scabra

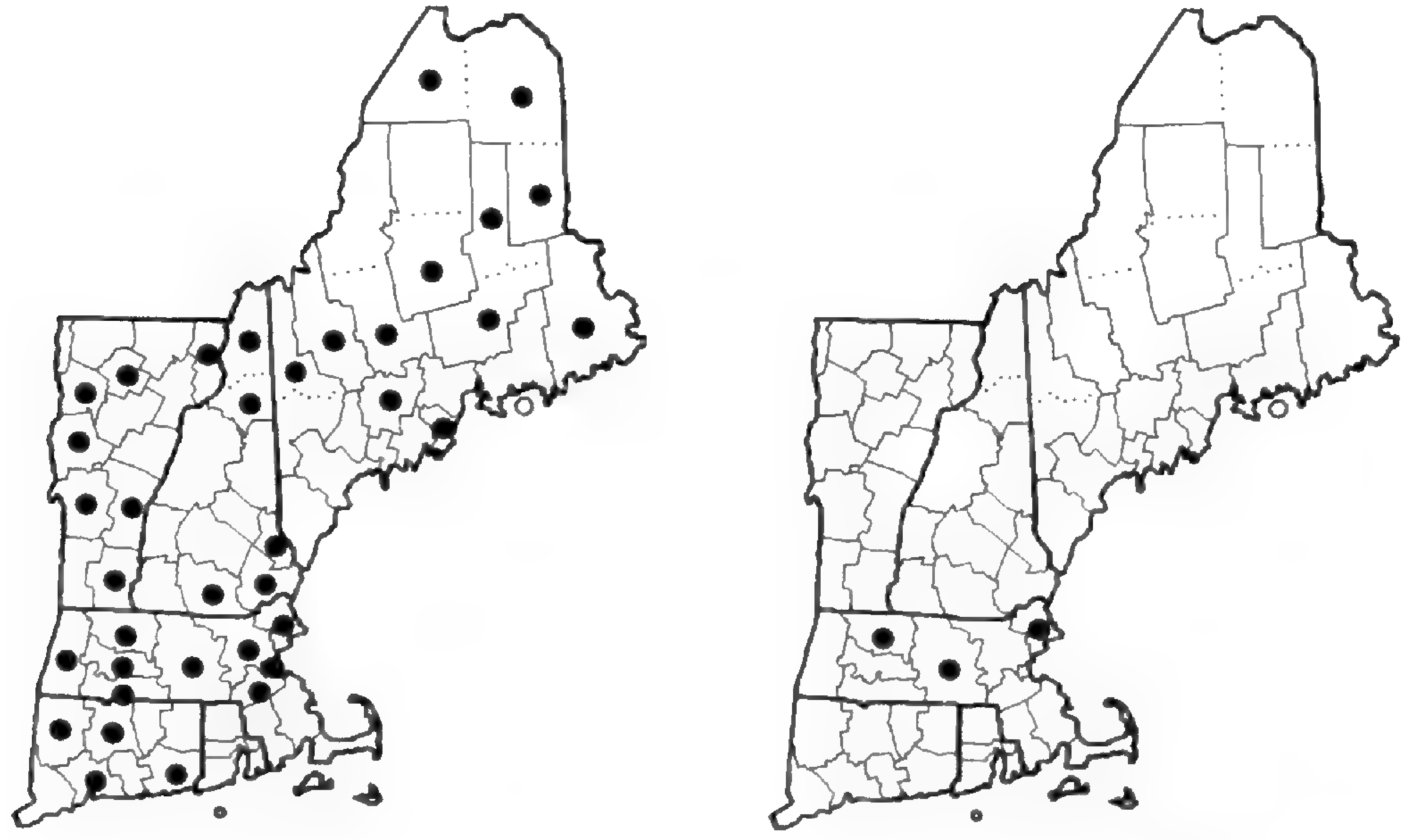
AGROSTIS STOLONIFERA

Figure 4. Distribution maps for *Agrostis mertensii, A. perennans, A. scabra* and *A. STOLONIFERA*.



AIRA CARYOPHYLLEA var. *CARYOPHYLLEA*

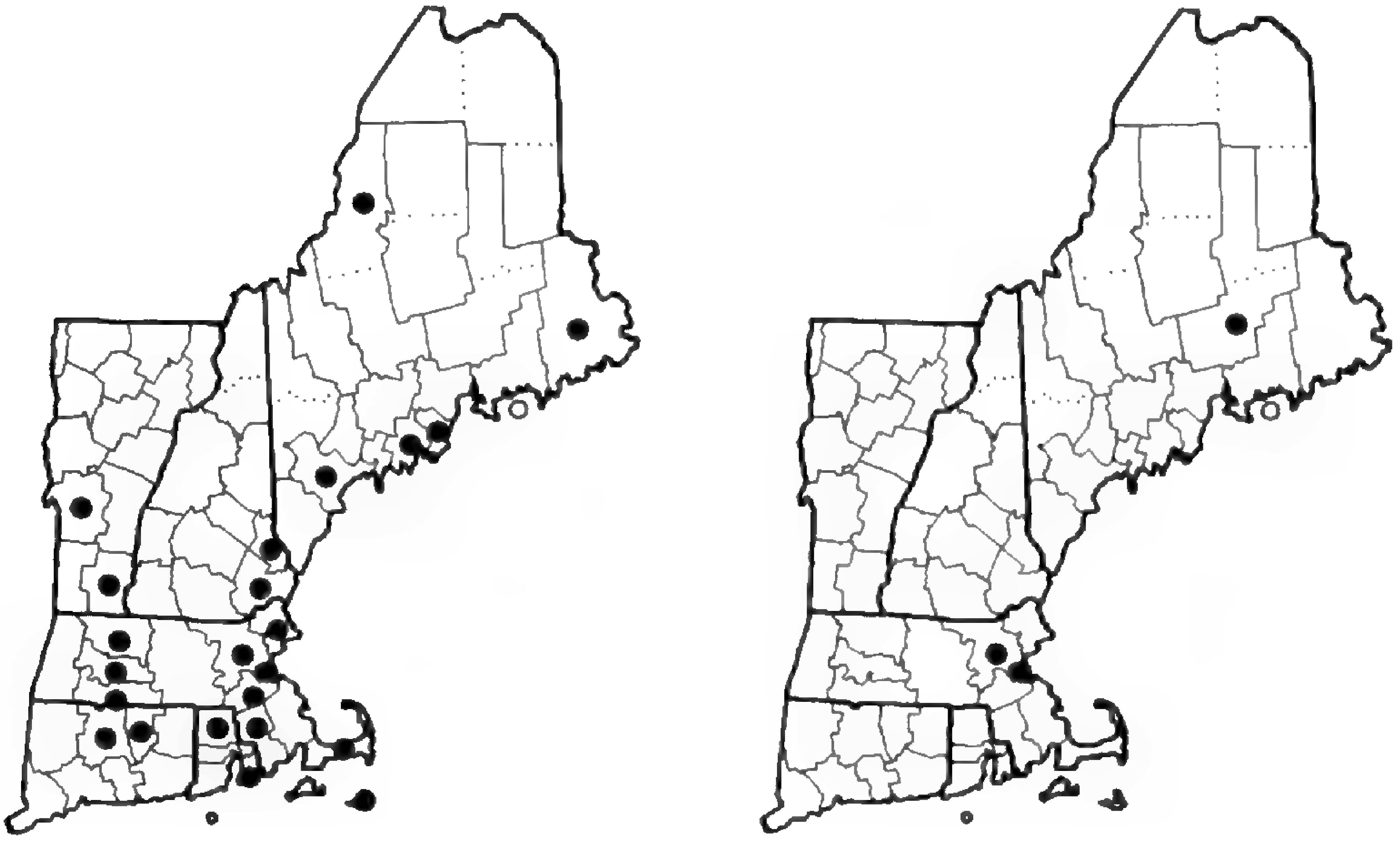
AIRA PRAECOX



Alopecurus aequalis

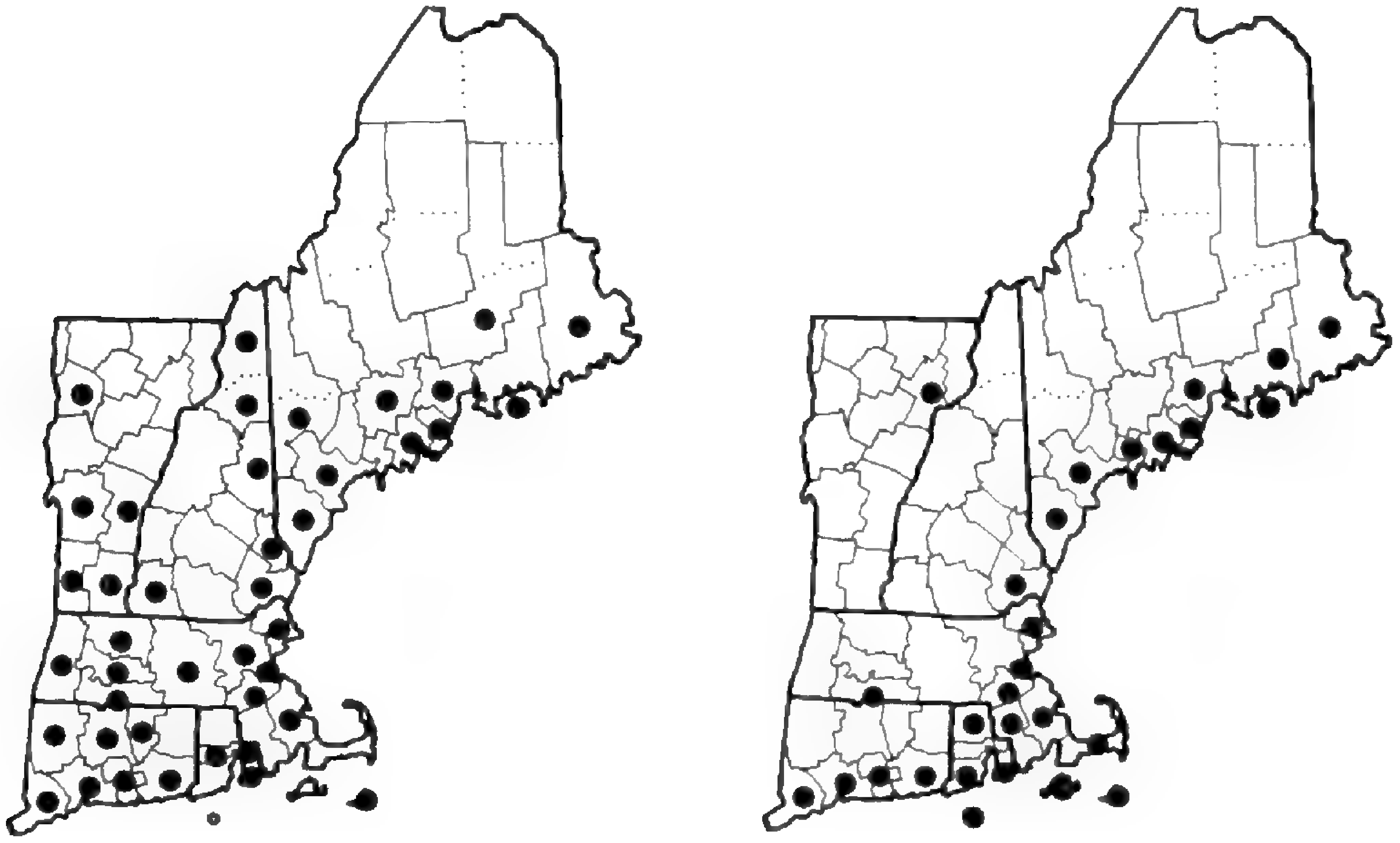
ALOPECURUS CAROLINIANUS

Figure 5. Distribution maps for *AIRA CARYOPHYLLEA* var. *CARYOPHYLLEA*, *A. PRAECOX*, *Alopecurus aequalis* and *A. CAROLINIANUS*.



ALOPECURUS GENICULATUS

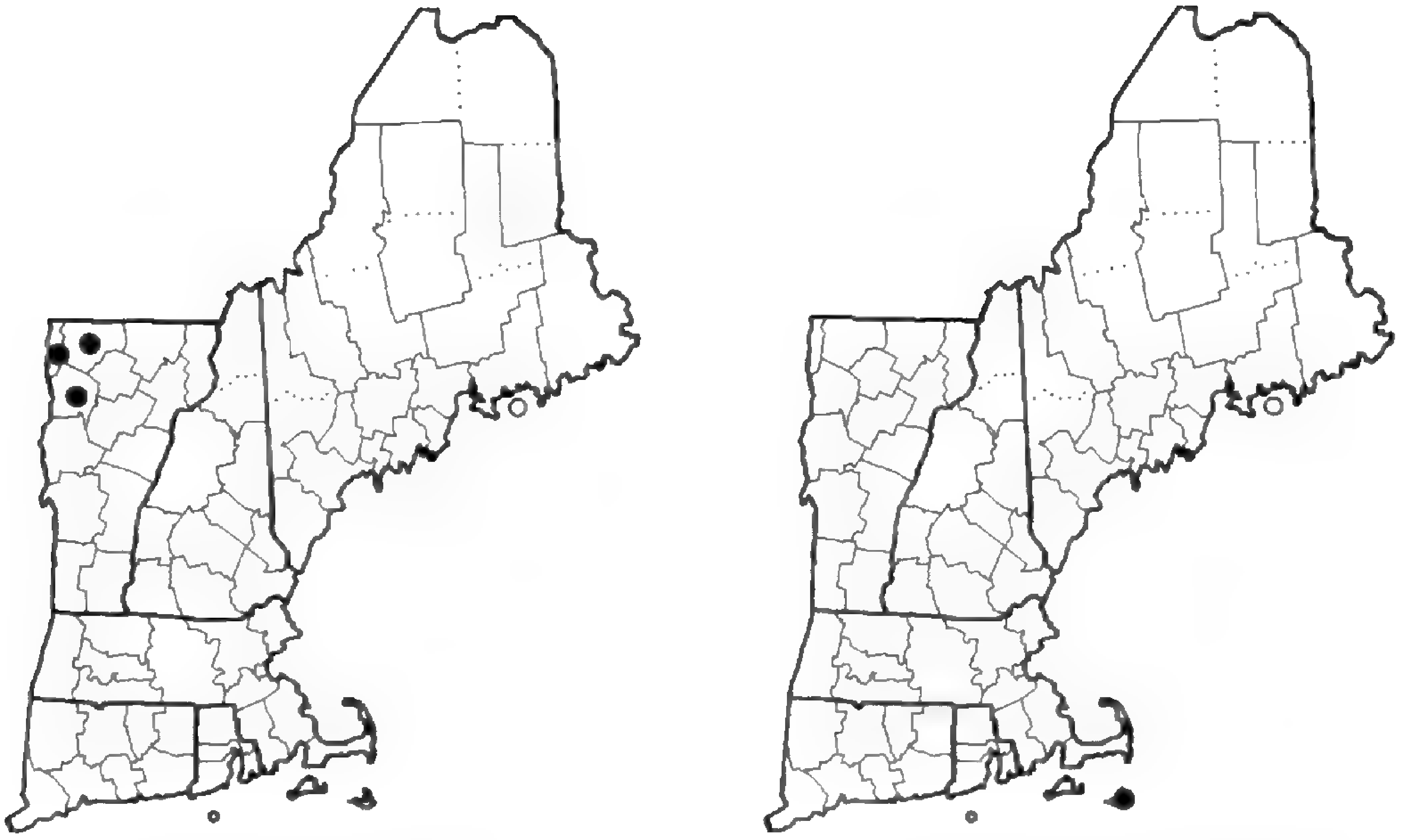
ALOPECURUS MYOSUROIDES



ALOPECURUS PRATENSIS

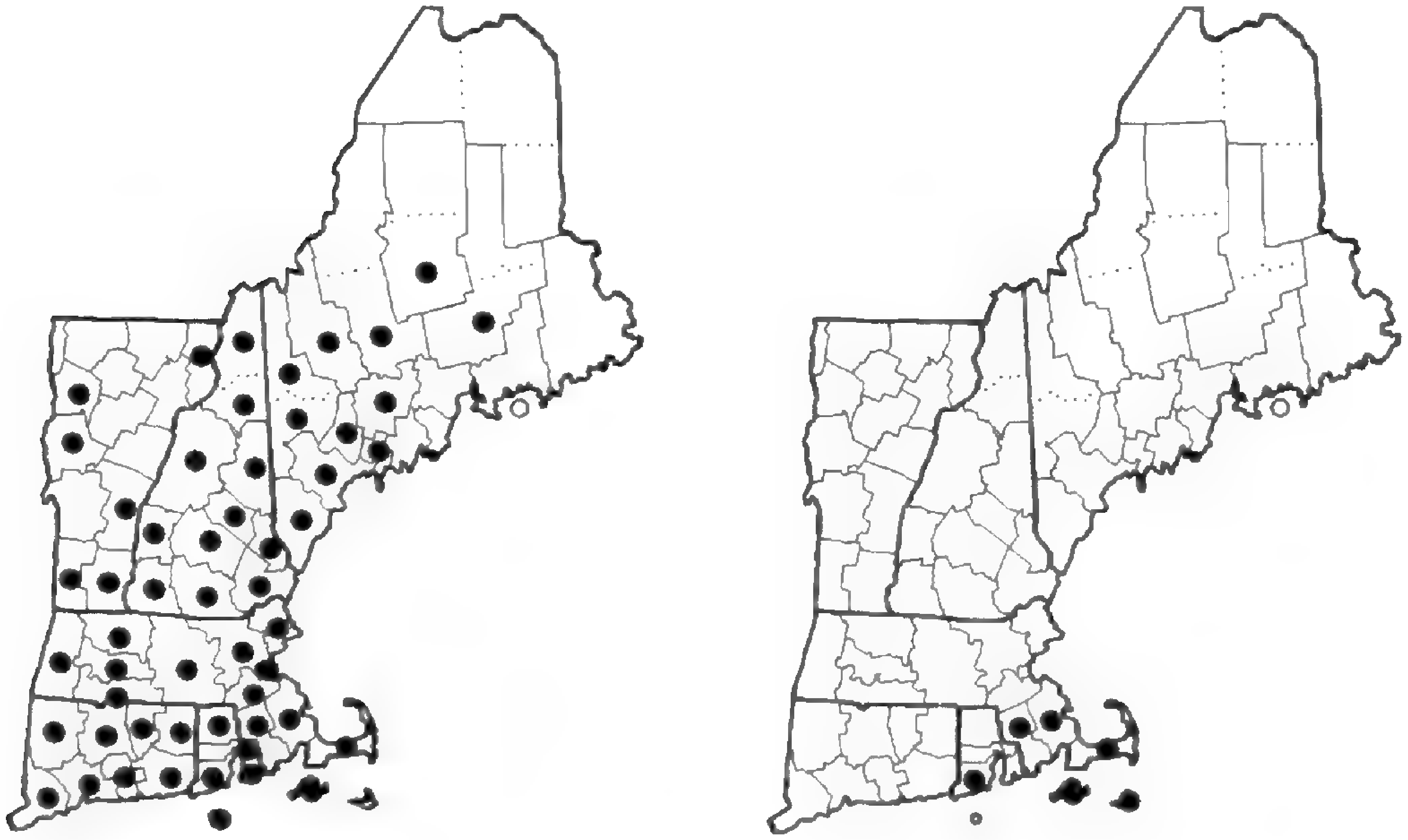
Ammophila breviligulata

Figure 6. Distribution maps for *ALOPECURUS GENICULATUS, A. MYOSUROIDES, A. PRATENSIS* and *Ammophila breviligulata.*



Ammophila champlainensis

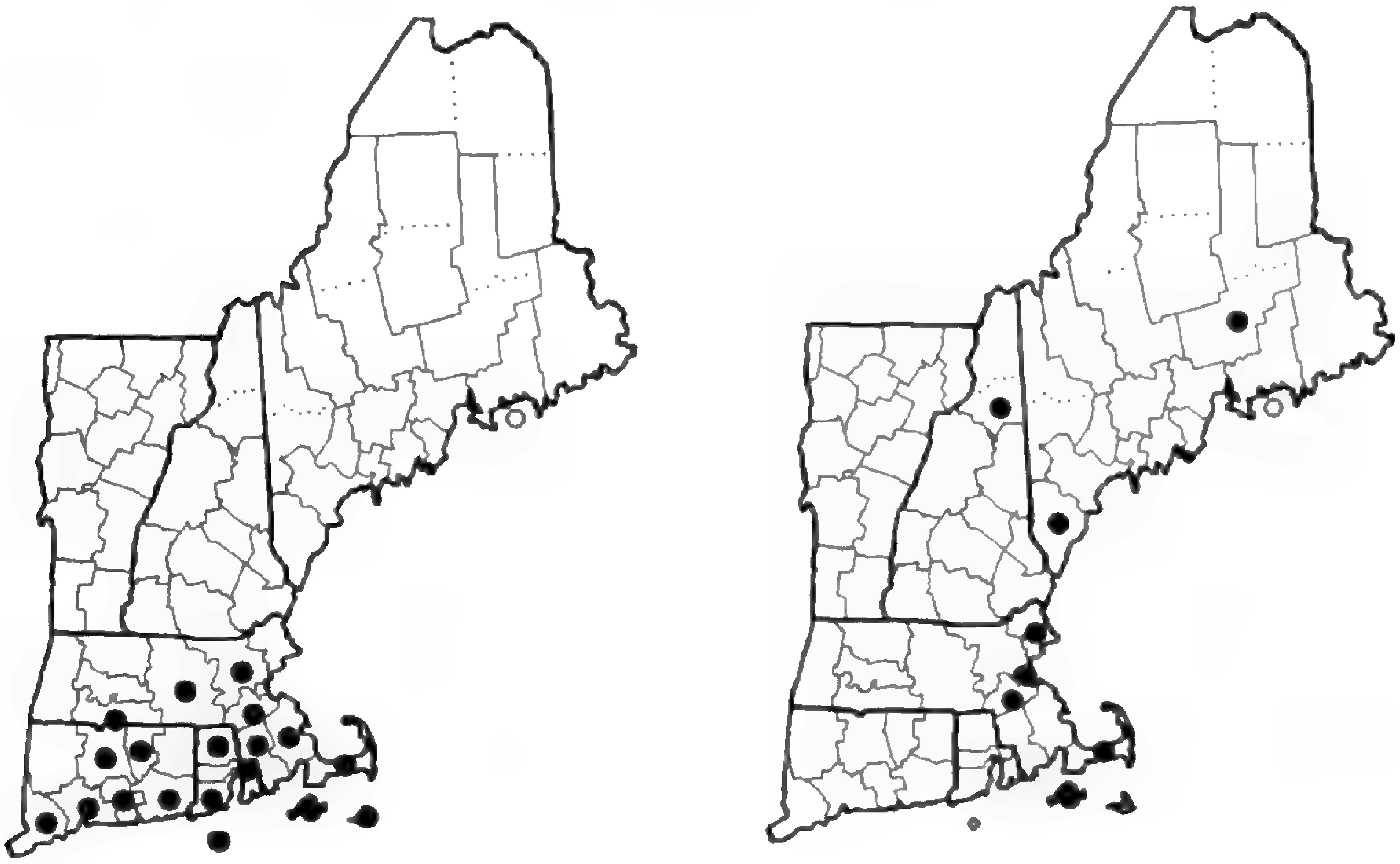
AMPHICARPUM PURSHII



Andropogon gerardii

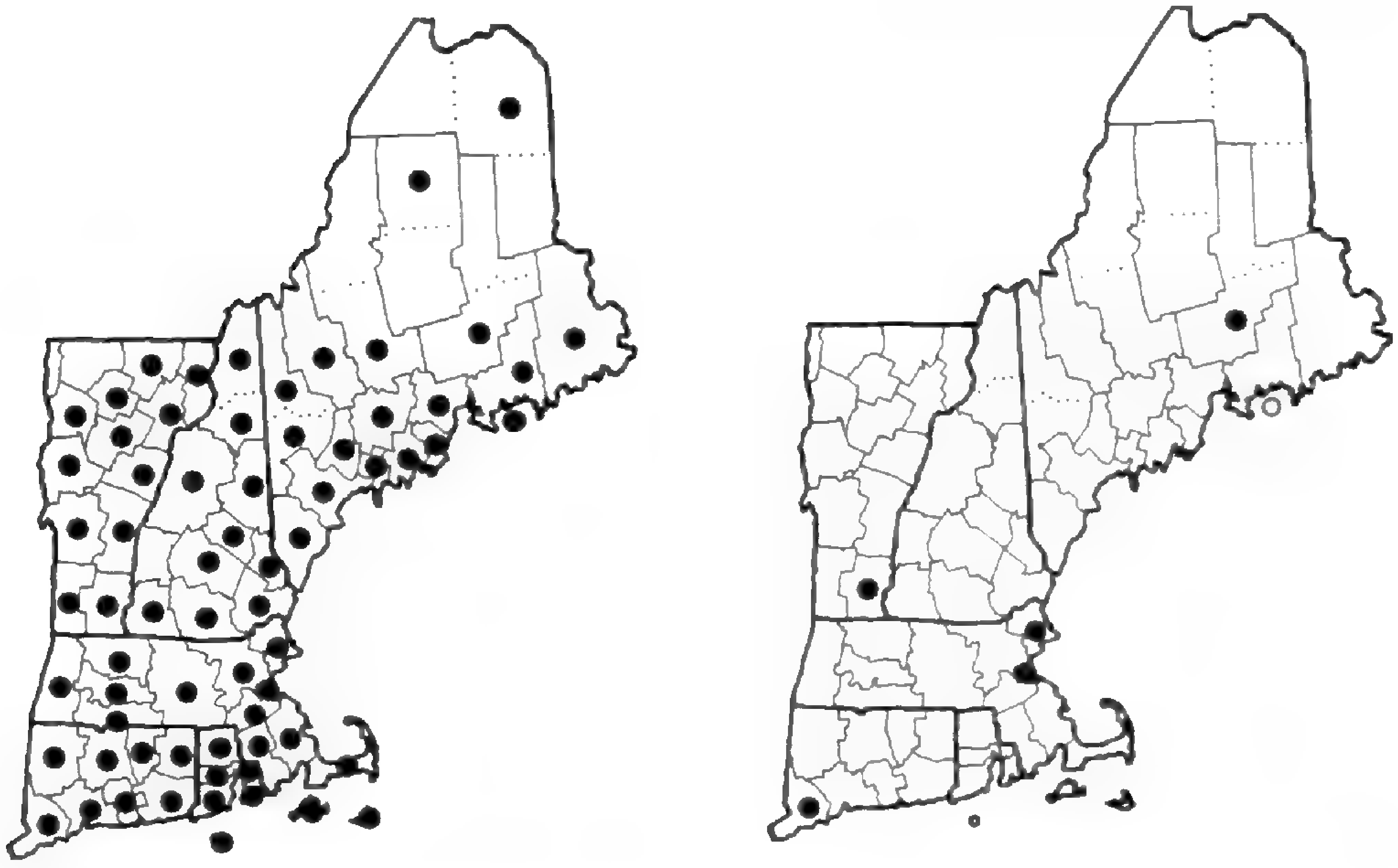
Andropogon glomeratus

Figure 7. Distribution maps for *Ammophila champlainensis*, *AMPHICARPUM PURSHII*, *Andropogon gerardii* and *A. glomeratus*.



Andropogon virginicus

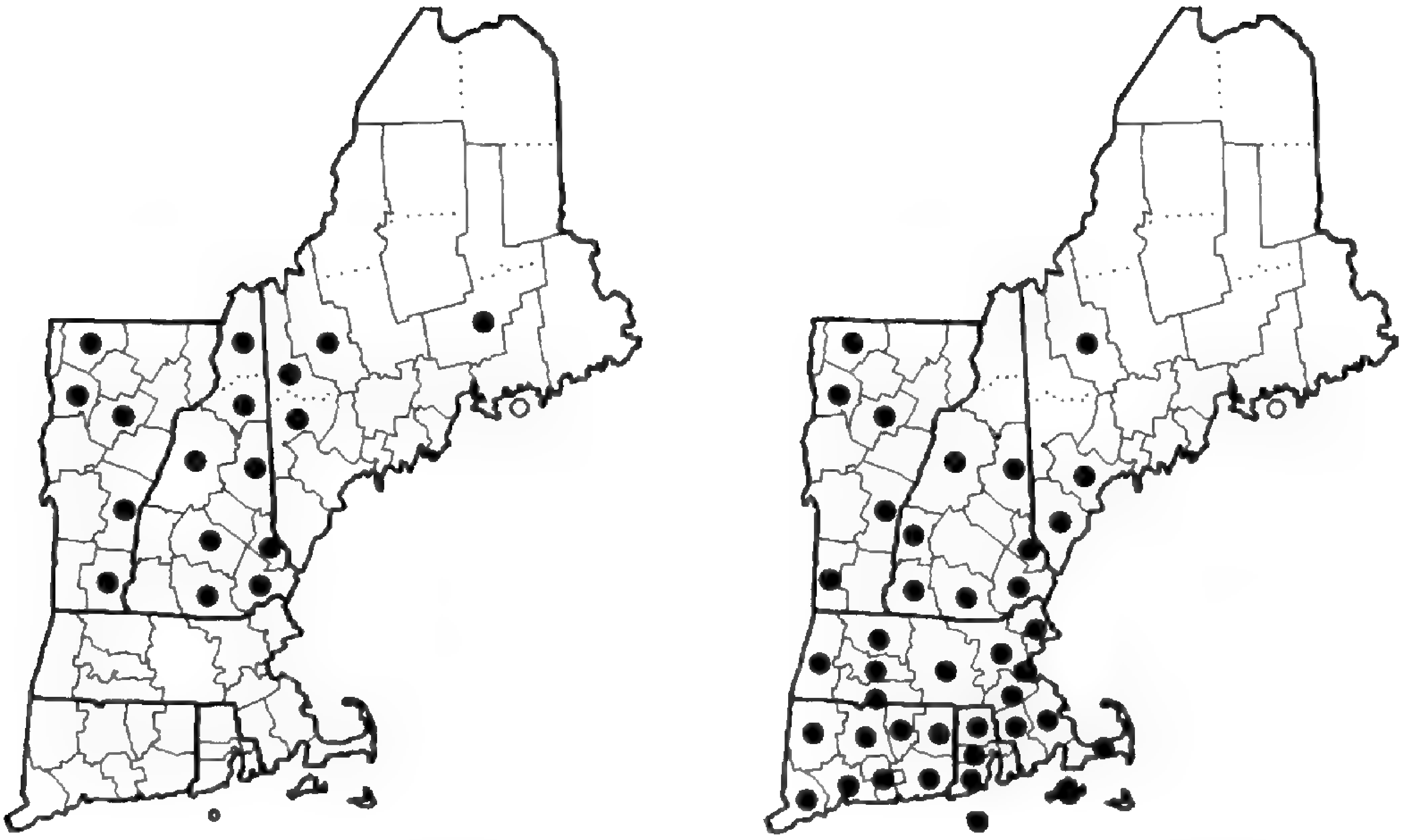
ANTHOXANTHUM ARISTATUM



ANTHOXANTHUM ODORATUM

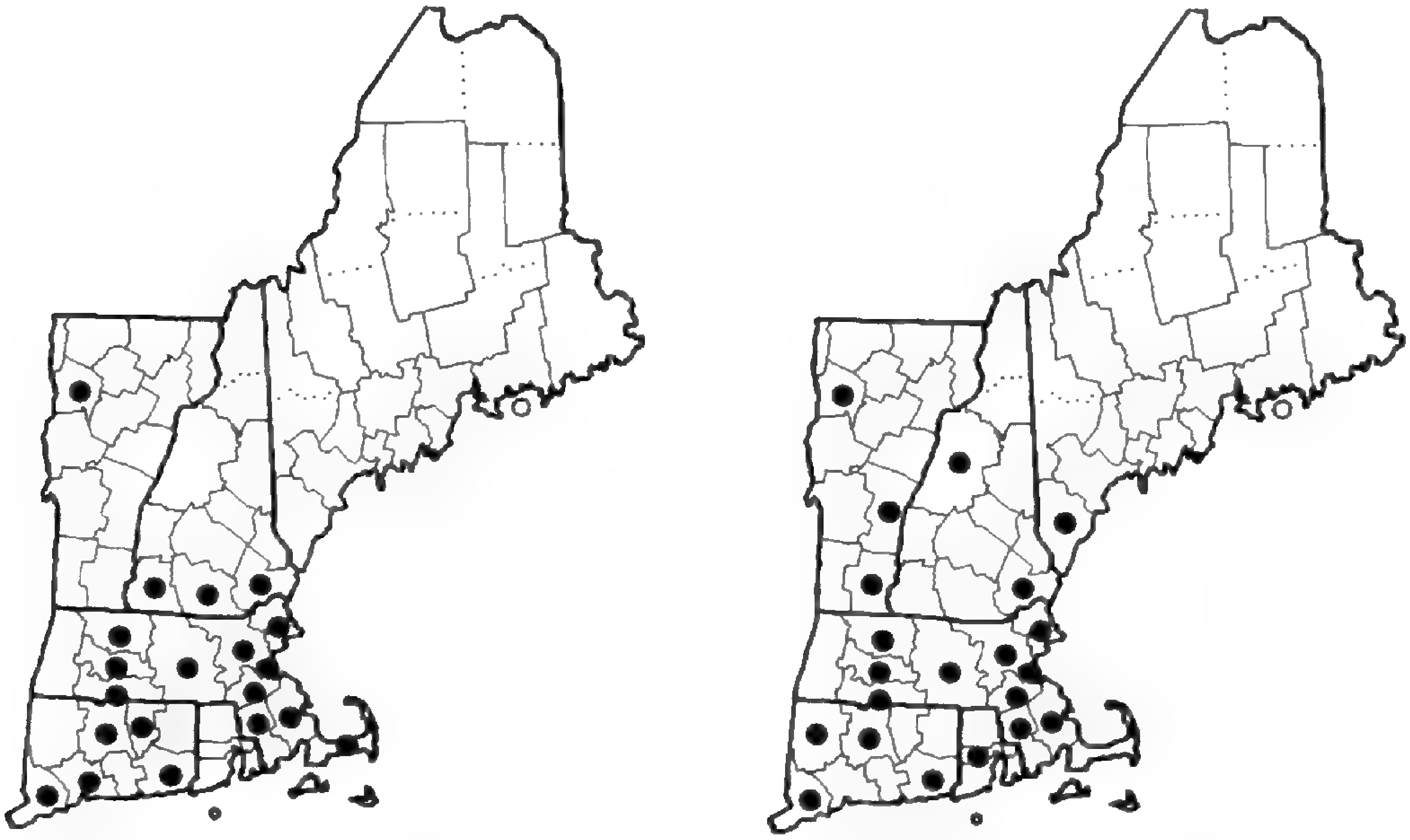
APERA SPICA-VENTI

Figure 8. Distribution maps for *Andropogon virginicus*, *ANTHOXANTHUM ARISTATUM*, *A. ODORATUM* and *APERA SPICA-VENTI*.



Aristida basiramea

Aristida dichotoma



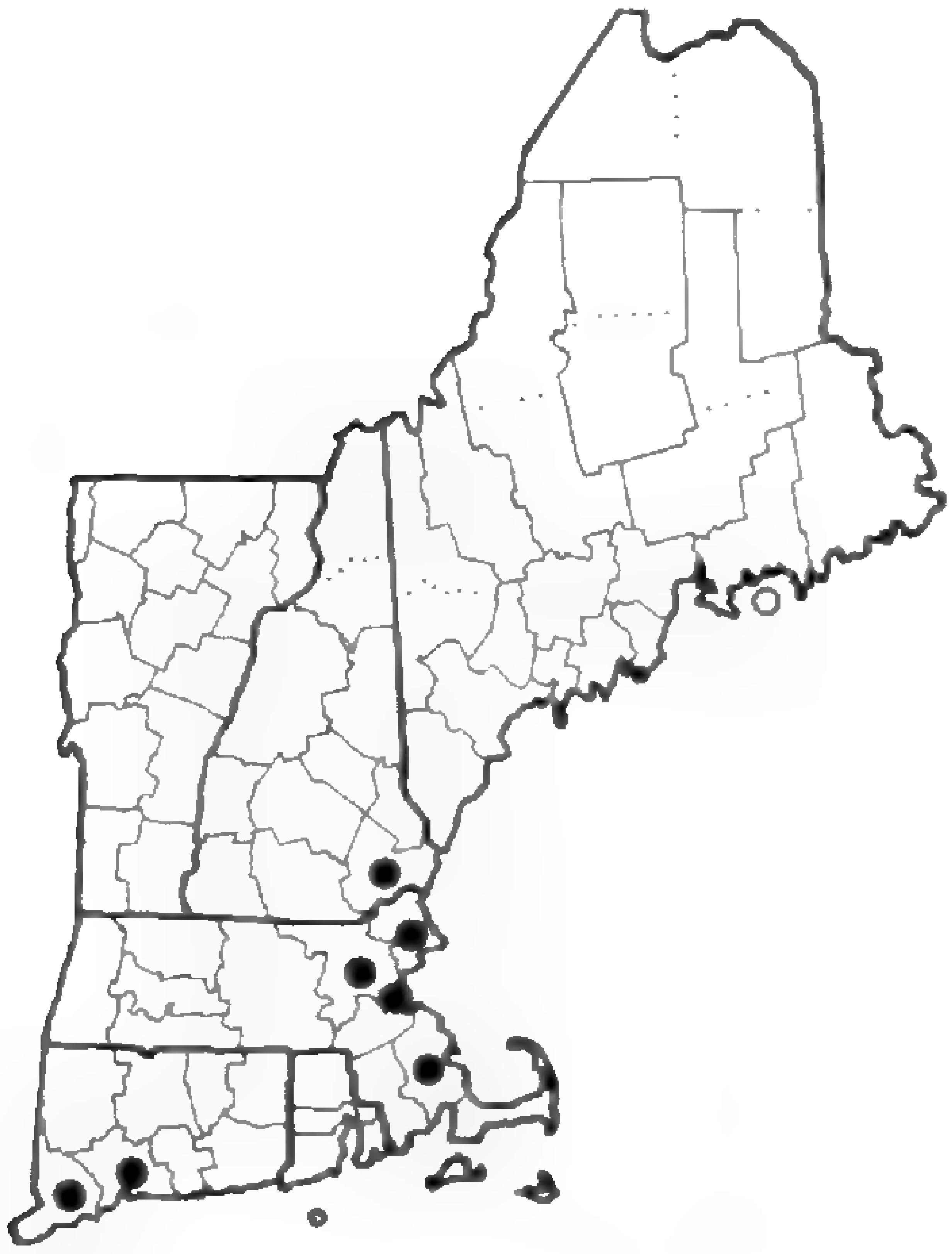
Aristida longespica
var. *geniculata*

Aristida oligantha

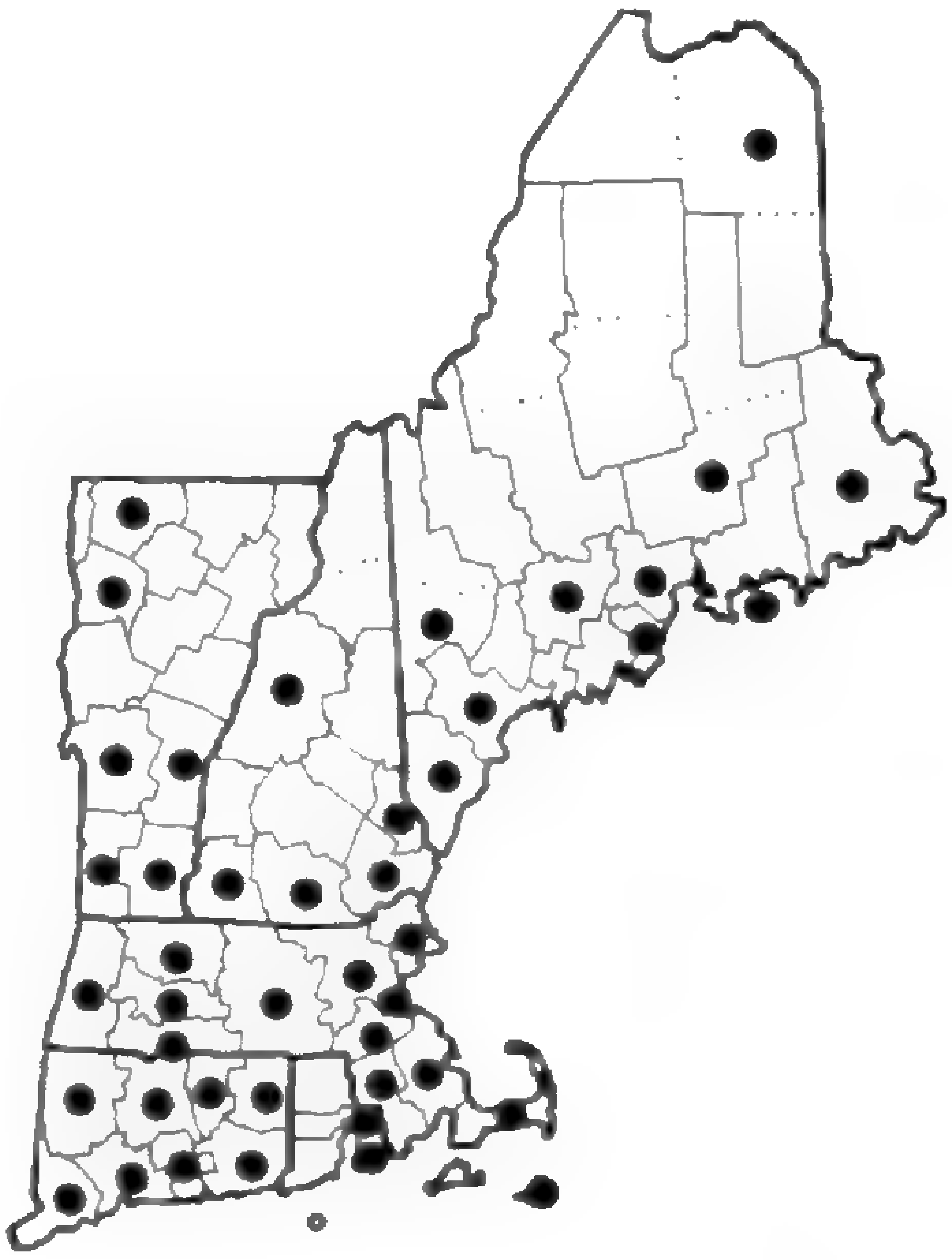
Figure 9. Distribution maps for *Aristida basiramea, A. dichotoma, A. longespica* var. *geniculata* and *A. oligantha.*

Aristida purpurascens

ARISTIDA PURPUREA var. *NEALLEYI*

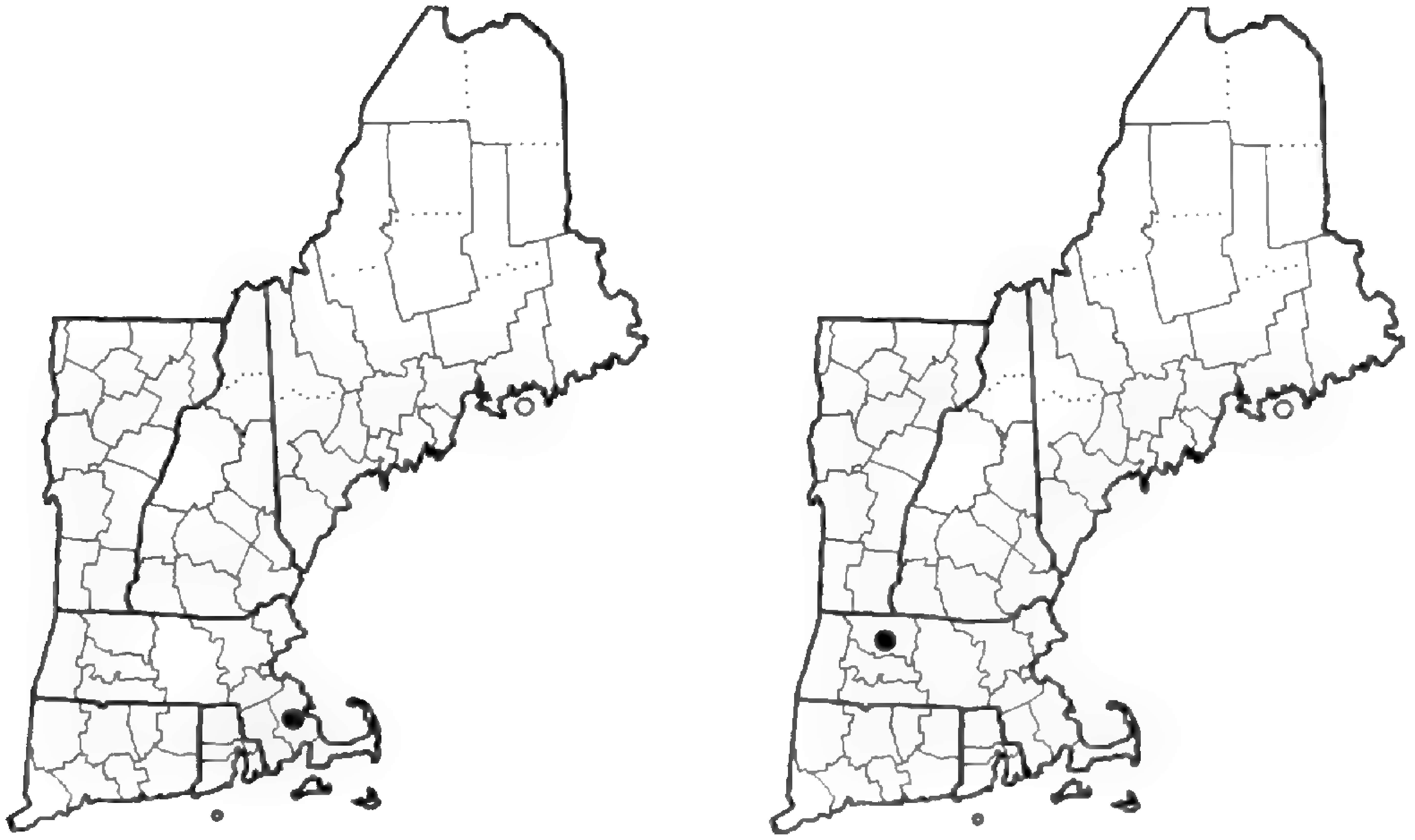


Aristida tuberculosa



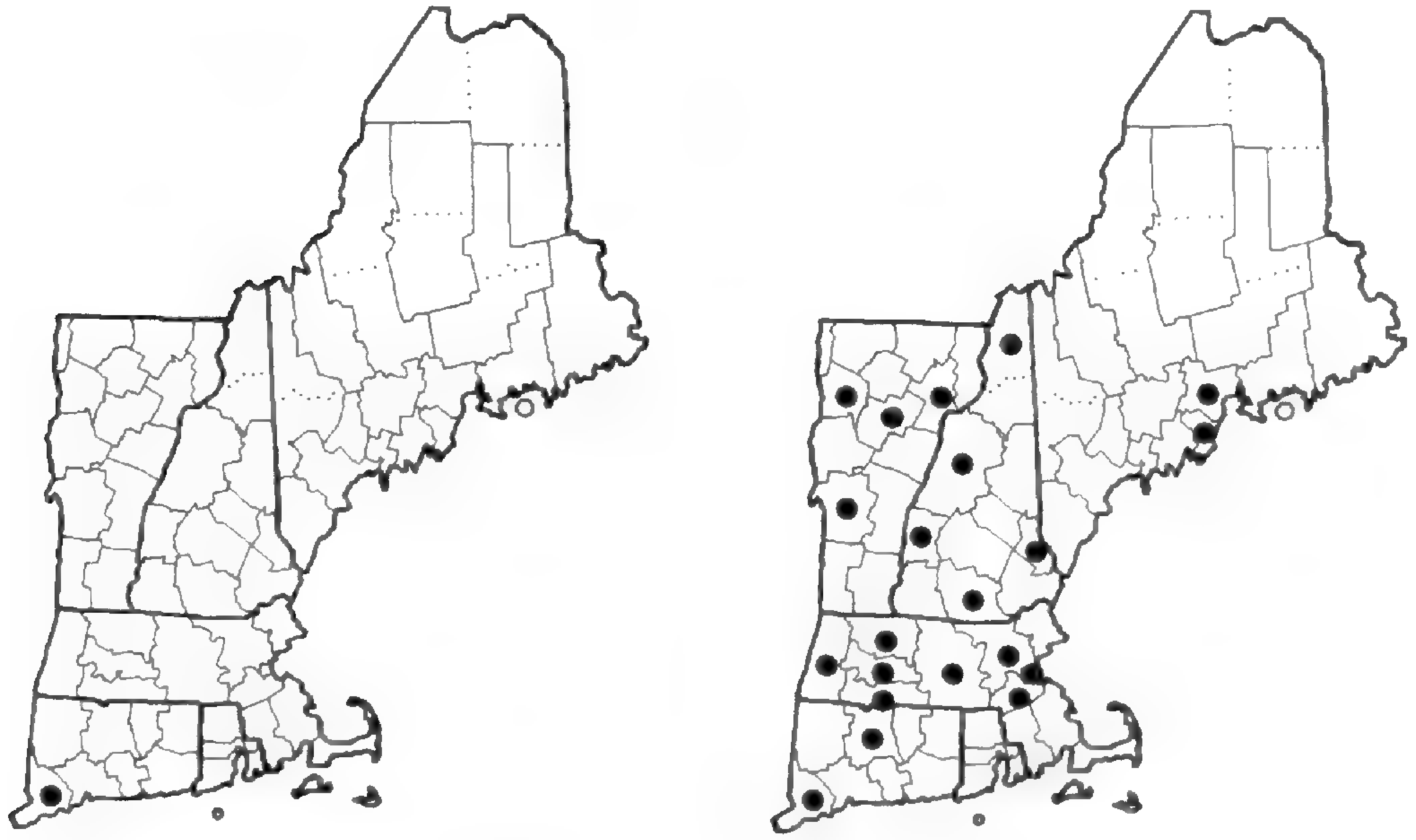
ARRHENATHERUM ELATIUS subsp. *ELATIUS*

Figure 10. Distribution maps for *Aristida purpurascens*, *A. PURPUREA* var. *NEALLEYI*, *A. tuberculosa* and *ARRHENATHERUM ELATIUS* subsp. *ELATIUS*.



ARRHENATHERUM ELATIUS
subsp. *BULBOSUM*

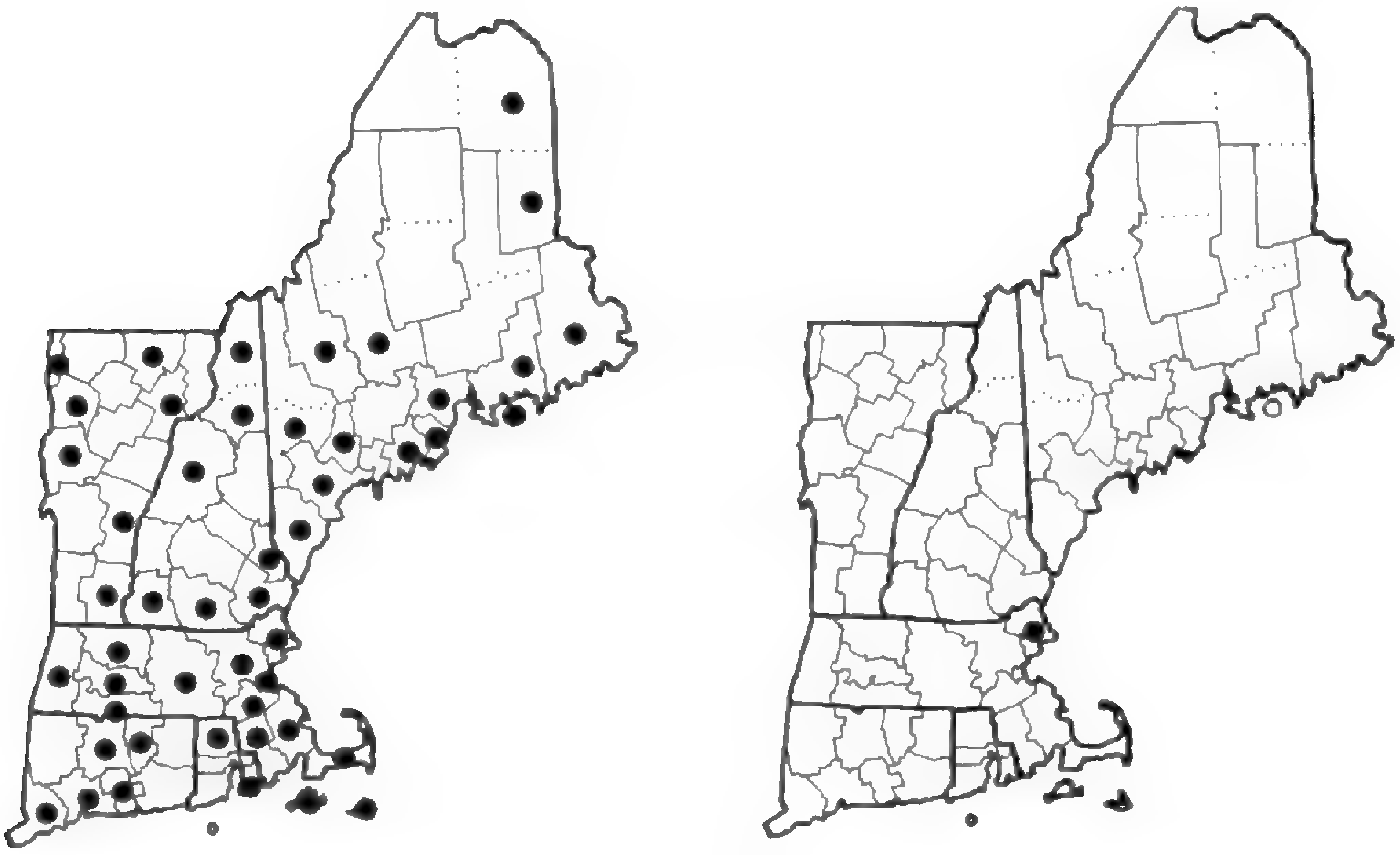
ARTHRAXON HISPIDUS



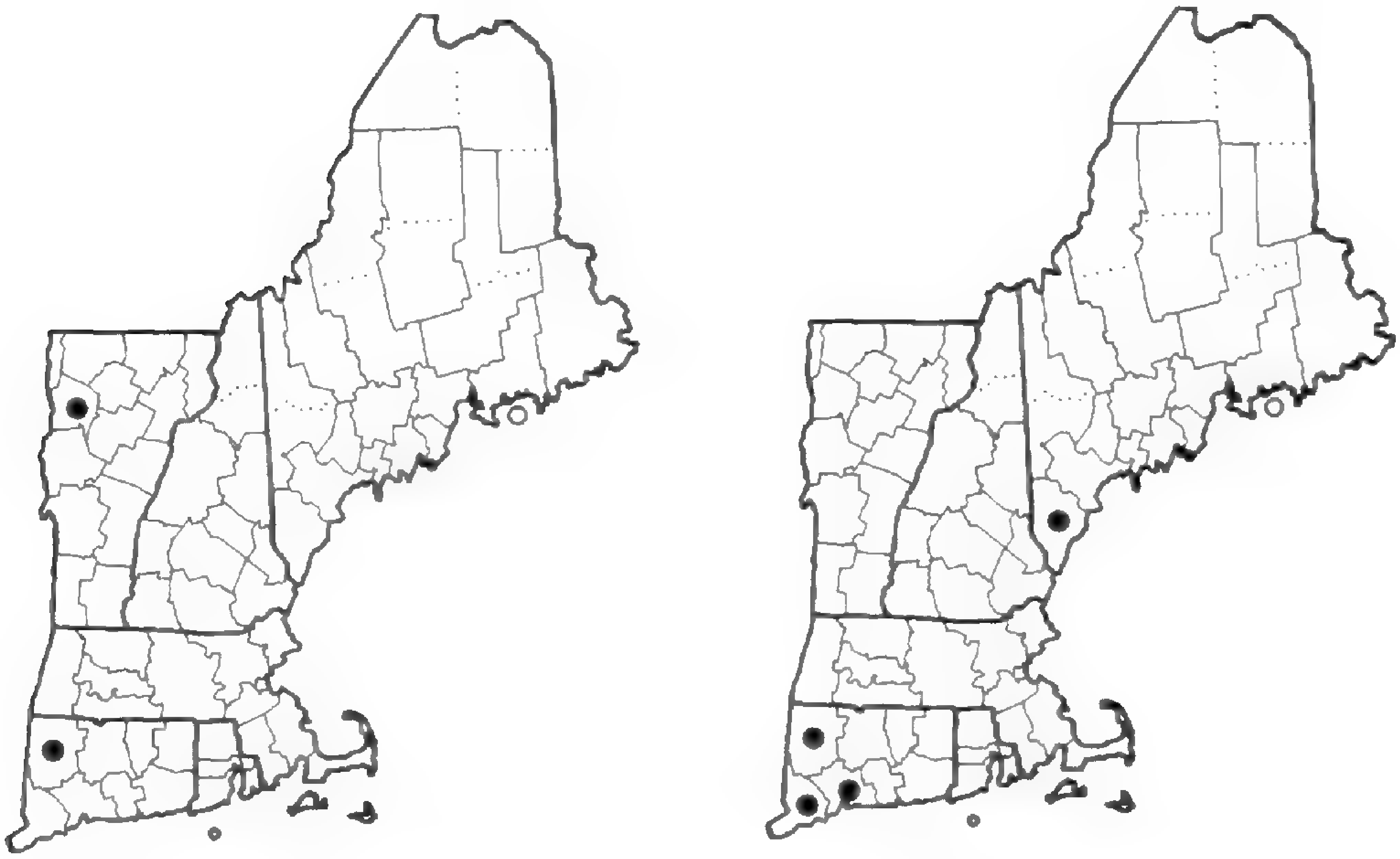
ARUNDINARIA JAPONICA

AVENA FATUA

Figure 11. Distribution maps for *ARRHENATHERUM ELATIUS* subsp. *BULBOSUM*, *ARTHRAXON HISPIDUS*, *ARUNDINARIA JAPONICA* and *AVENA FATUA*.

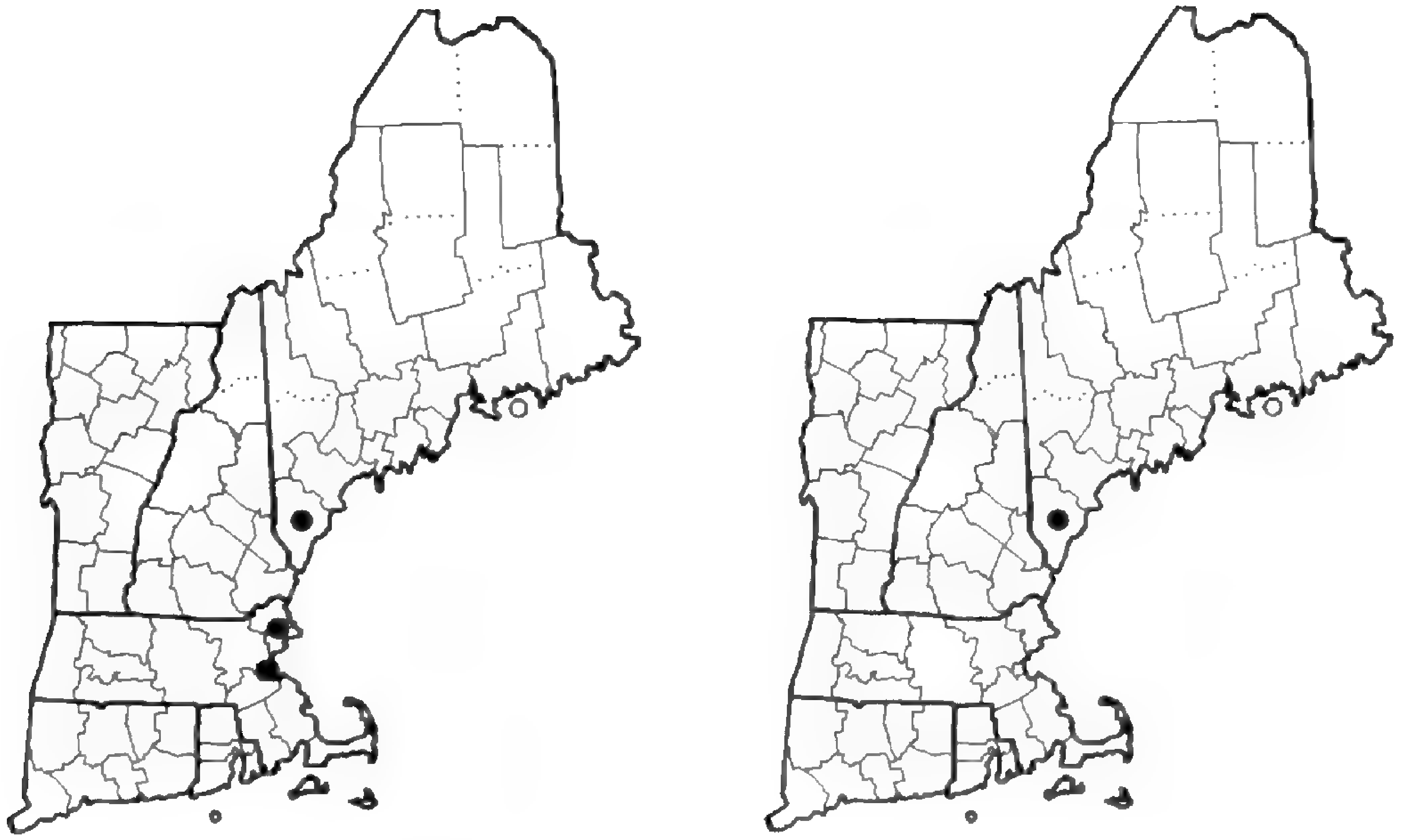


AVENA SATIVA *AVENA STRIGOSA*

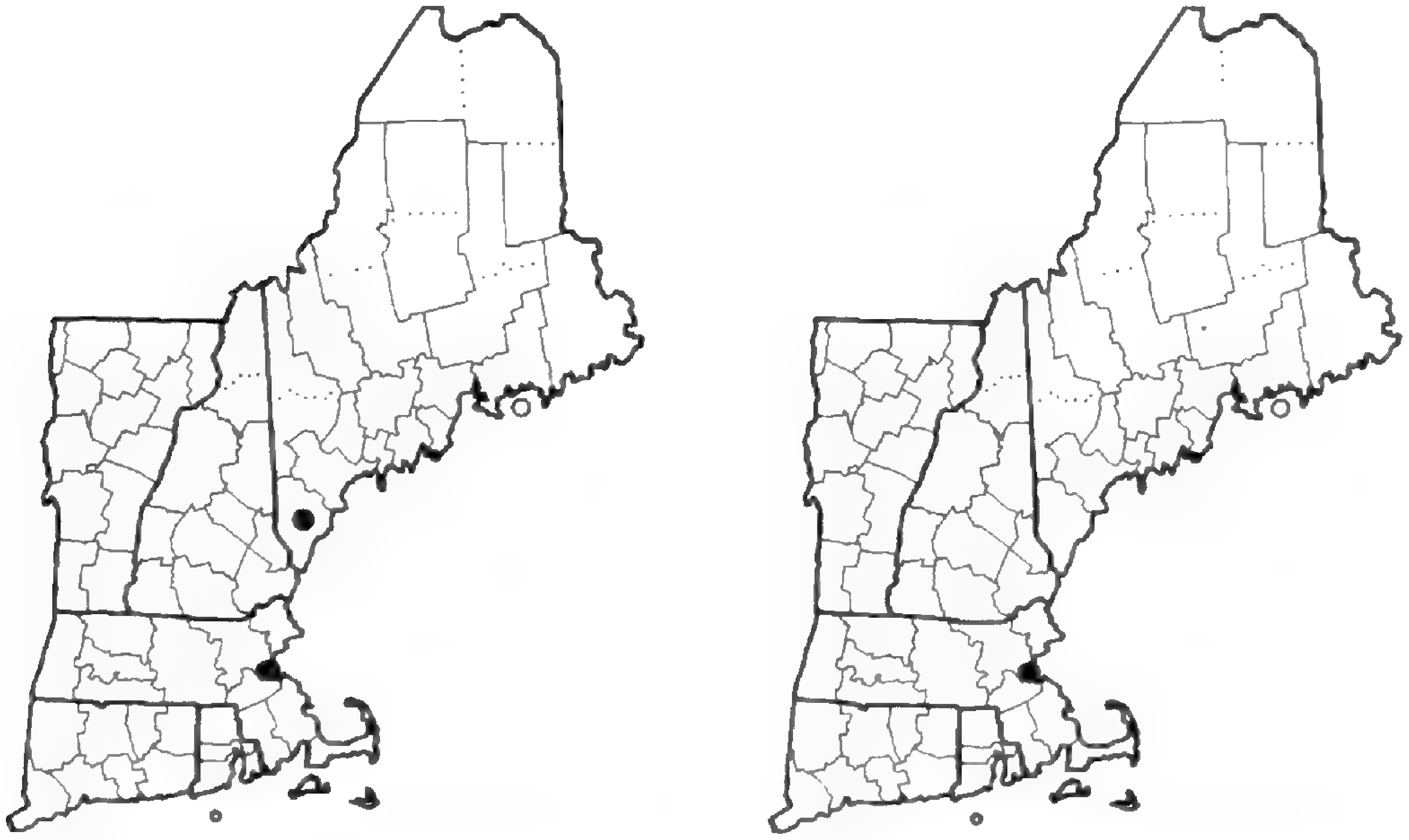


AVENULA PUBESCENS ***Bouteloua curtipendula***

Figure 12. Distribution maps for *AVENA SATIVA, A. STRIGOSA, AVENULA PUBESCENS* and *Bouteloua curtipendula.*

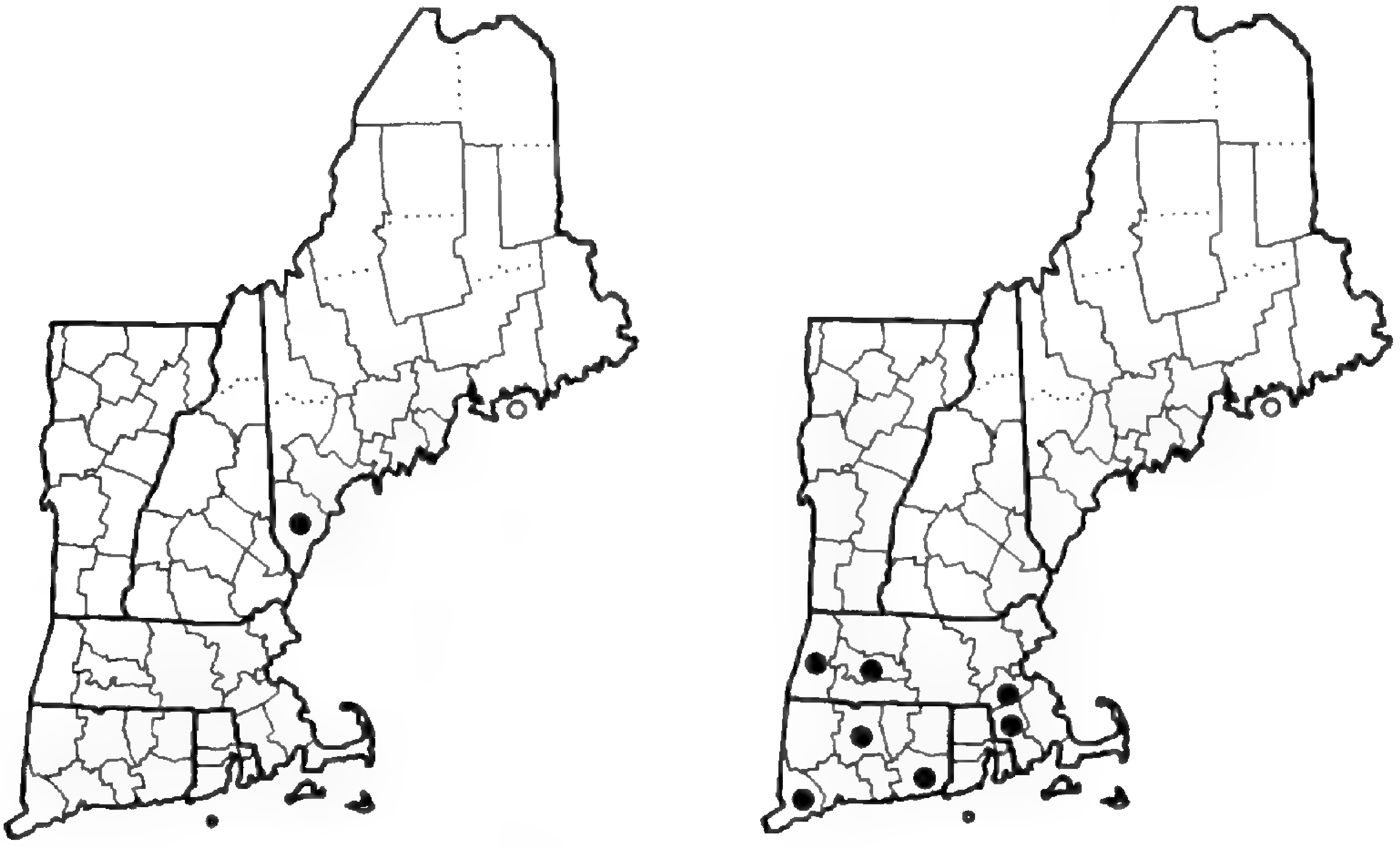


BOUTELOUA GRACILIS *BOUTELOUA HIRSUTA*



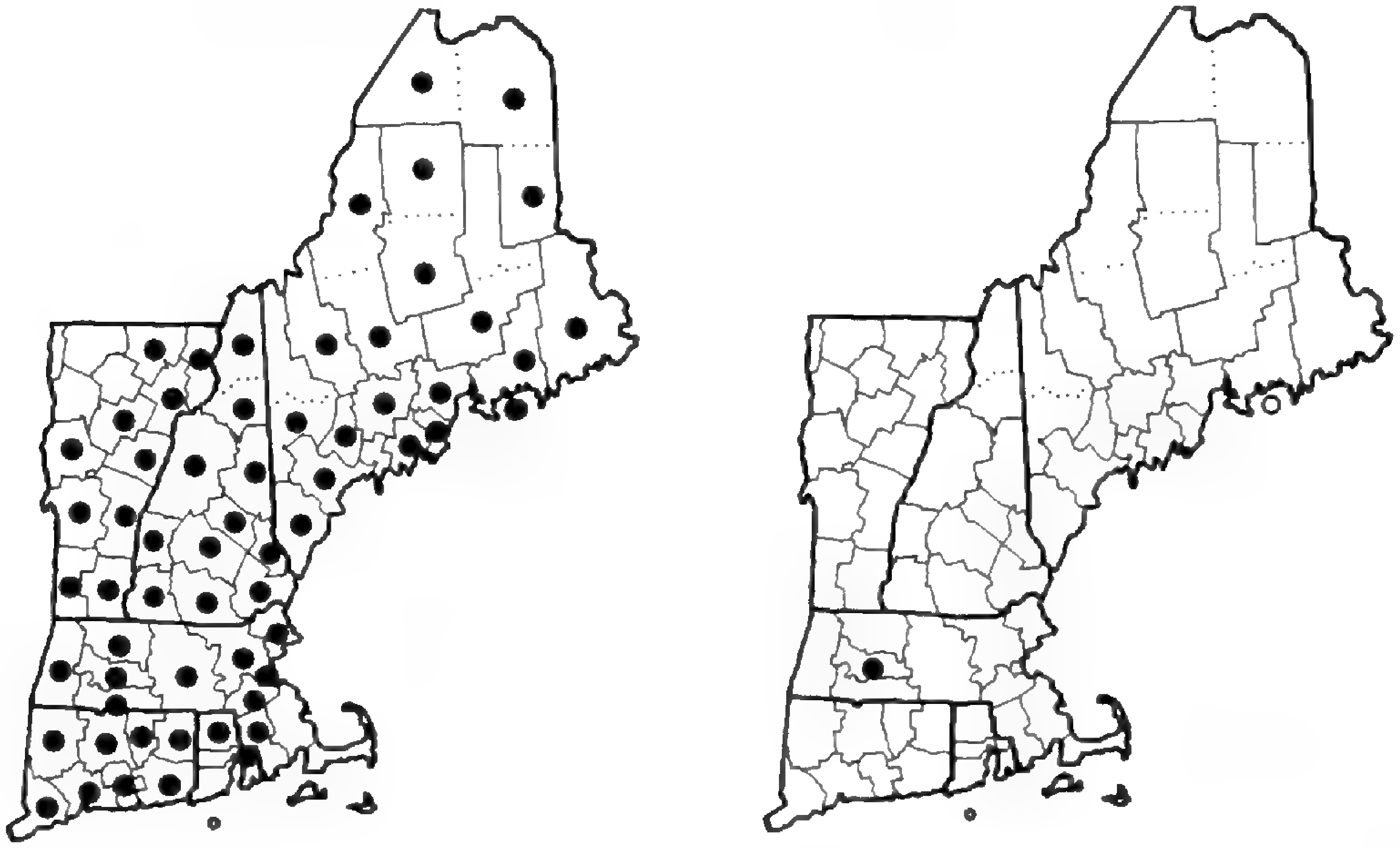
BOUTELOUA REPENS *BOUTELOUA RIGIDISETA*

Figure 13. Distribution maps for *BOUTELOUA GRACILIS, B. HIRSUTA, B. REPENS* and *B. RIGIDISETA*.



BOUTELOUA SIMPLEX

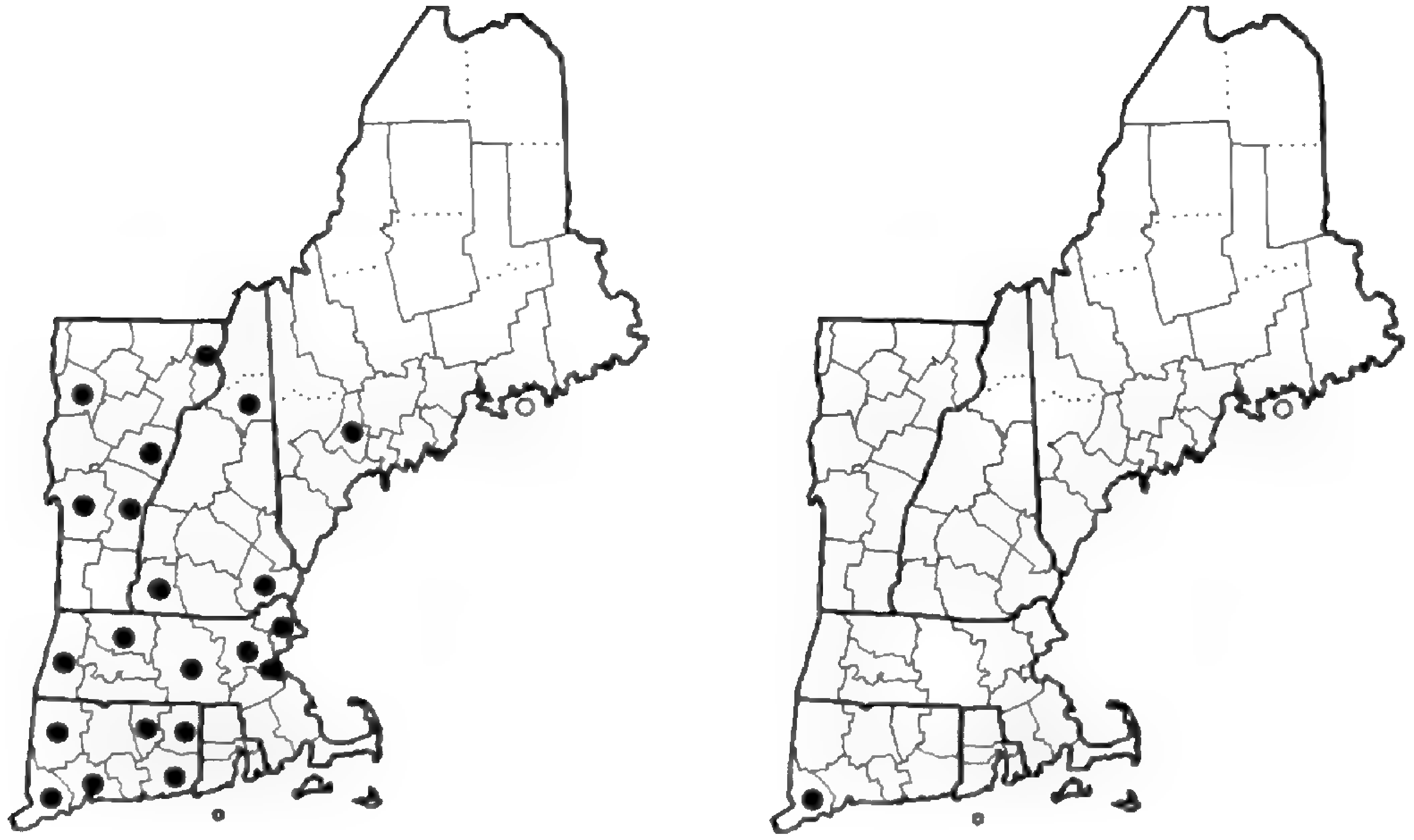
Brachyelytrum erectum
var. *erectum*



Brachyelytrum erectum
var. *glabratum*

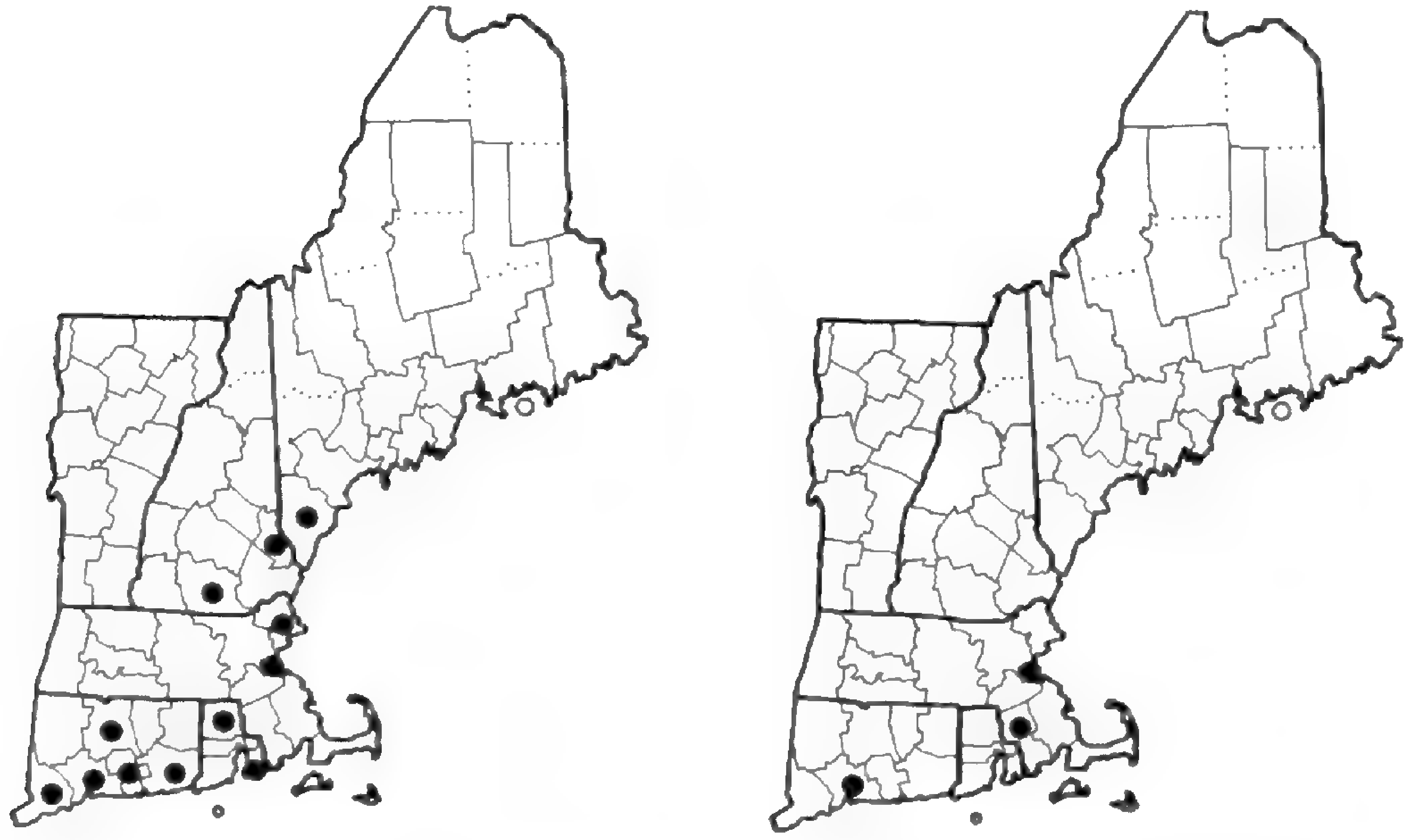
BRACHYPODIUM PINNATUM

Figure 14. Distribution maps for *BOUTELOUA SIMPLEX, Brachyelytrum erectum* var. *erectum, B. erectum* var. *glabratum* and *BRACHYPODIUM PINNATUM.*



BRIZA MEDIA

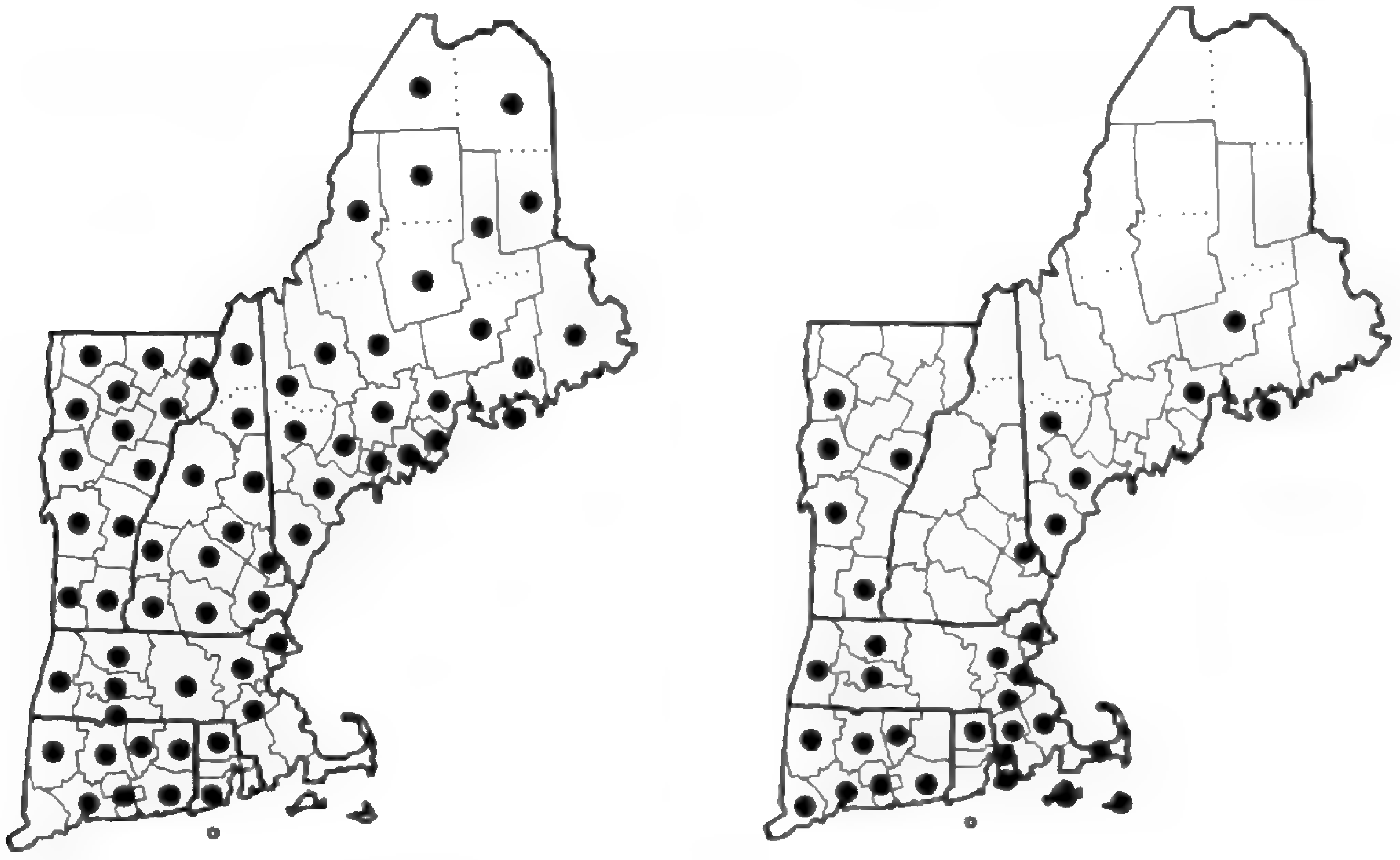
BRIZA MINOR



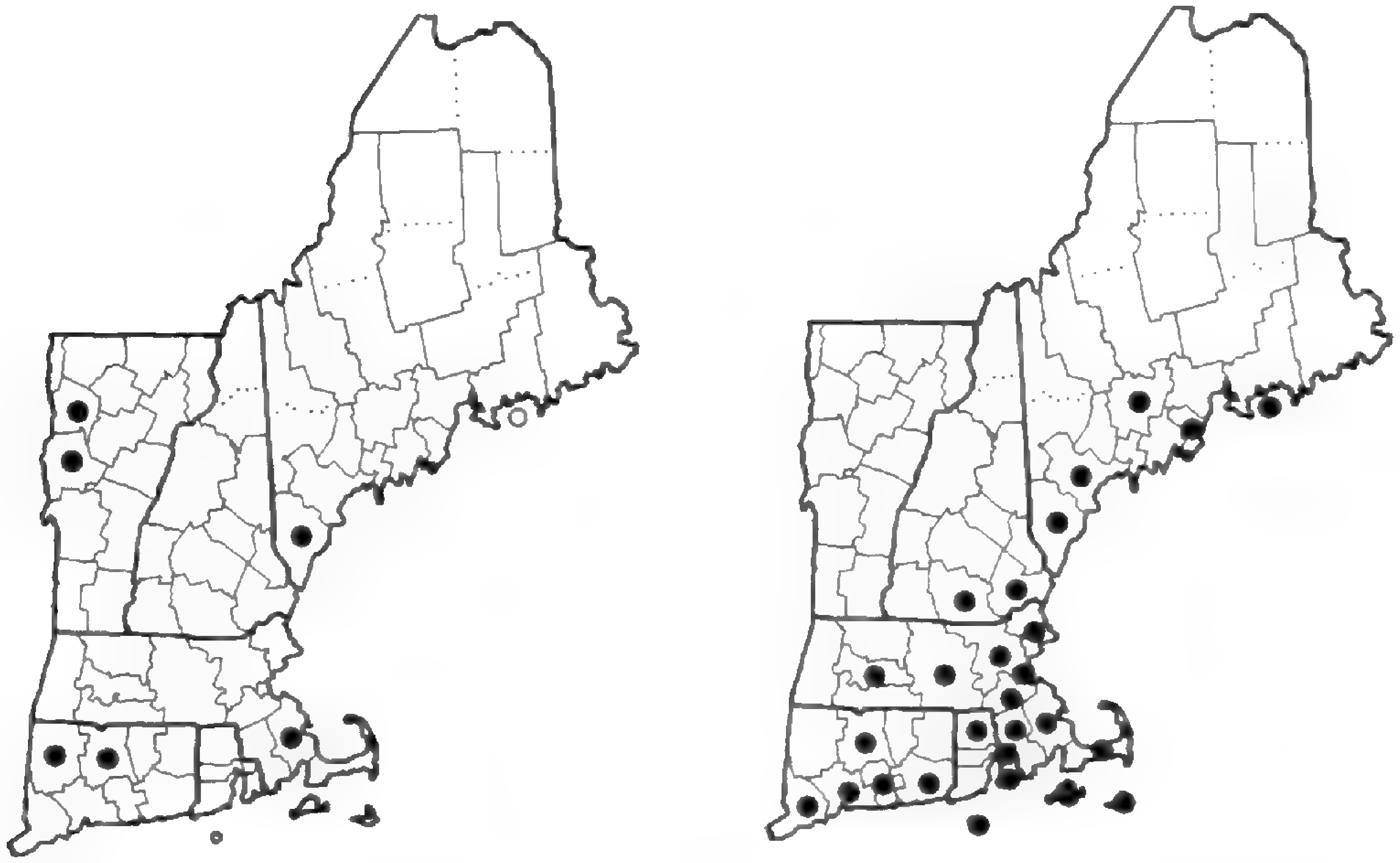
BROMUS ARVENSIS

BROMUS BRIZIFORMIS

Figure 15. Distribution maps for *BRIZA MEDIA, B. MINOR, BROMUS ARVENSIS* and *B. BRIZIFORMIS.*

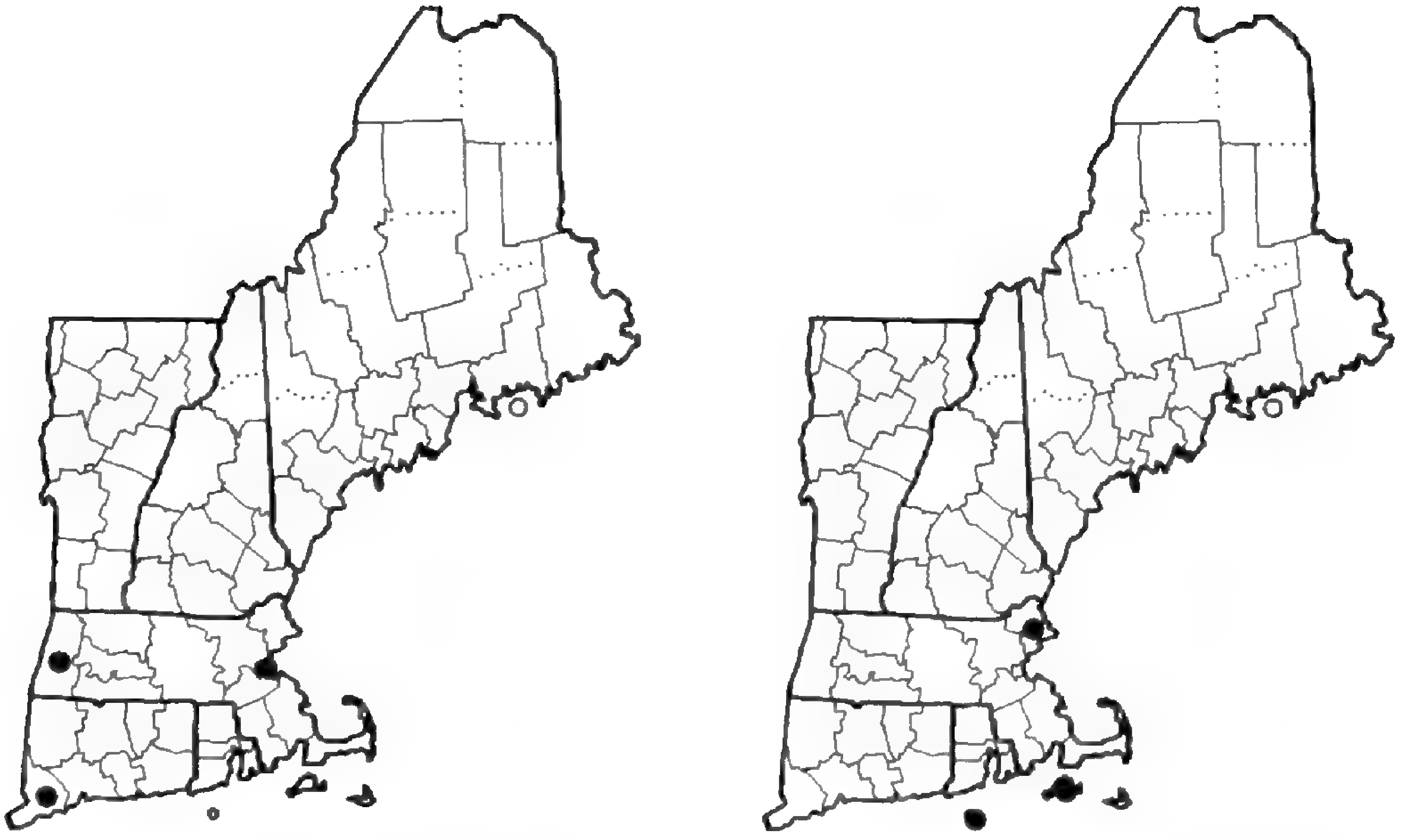


Bromus ciliatus BROMUS COMMUTATUS



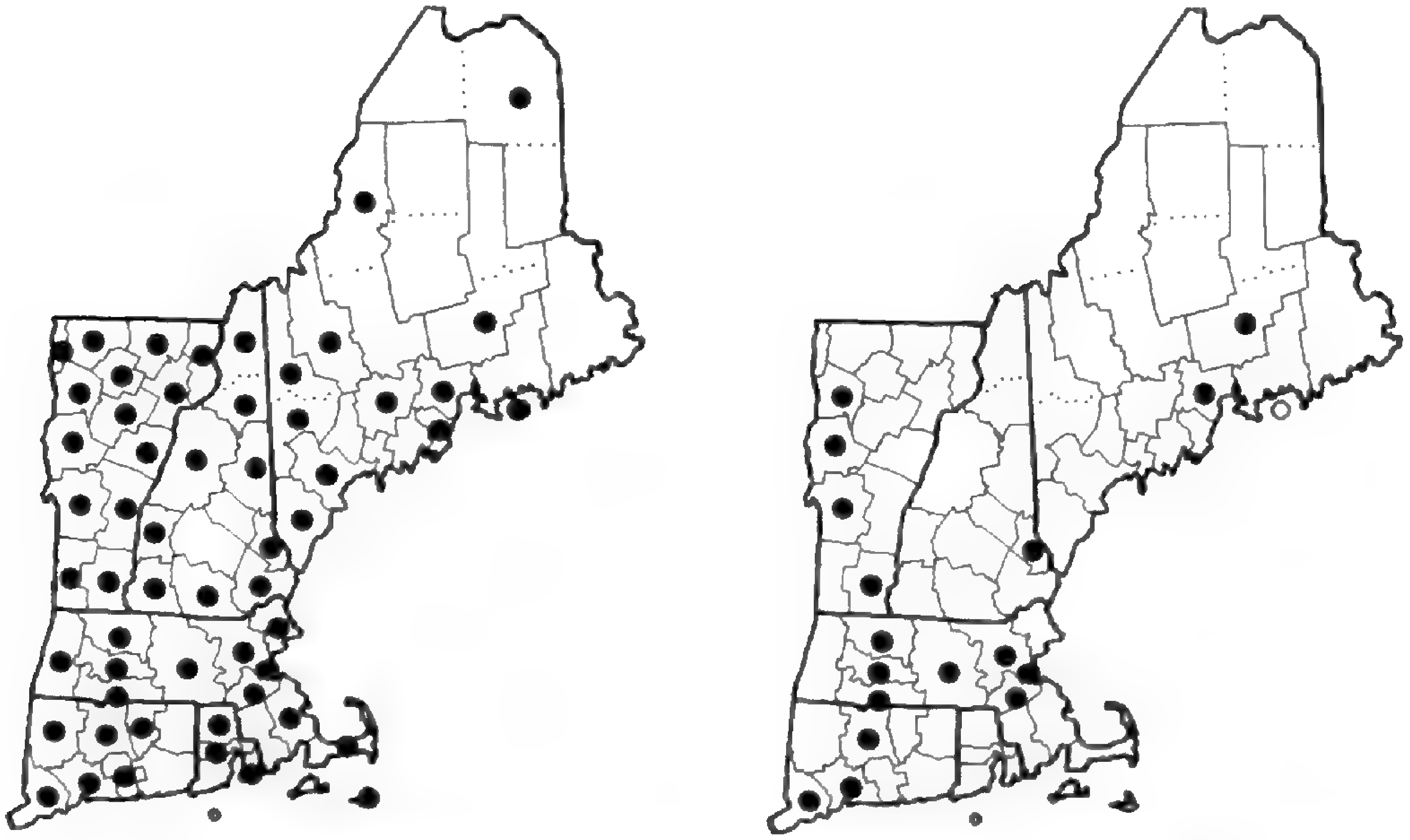
BROMUS ERECTUS BROMUS HORDEACEUS subsp. HORDEACEUS

Figure 16. Distribution maps for *Bromus ciliatus*, *B. COMMUTATUS*, *B. ERECTUS* and *B. HORDEACEUS* subsp. *HORDEACEUS*.



BROMUS HORDEACEUS subsp. *PSEUDOTHOMINEI*

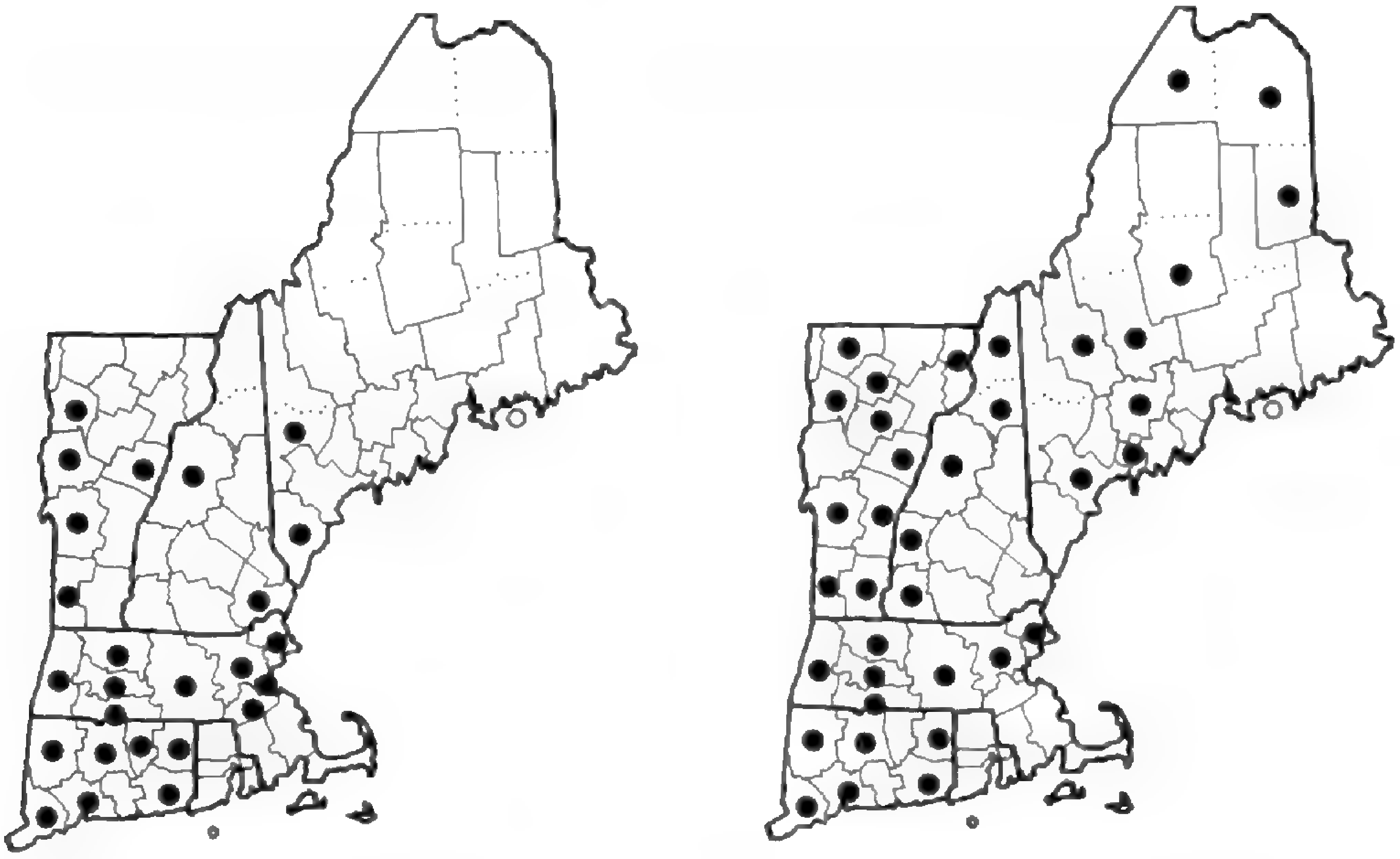
BROMUS HORDEACEUS subsp. *THOMINEI*



BROMUS INERMIS

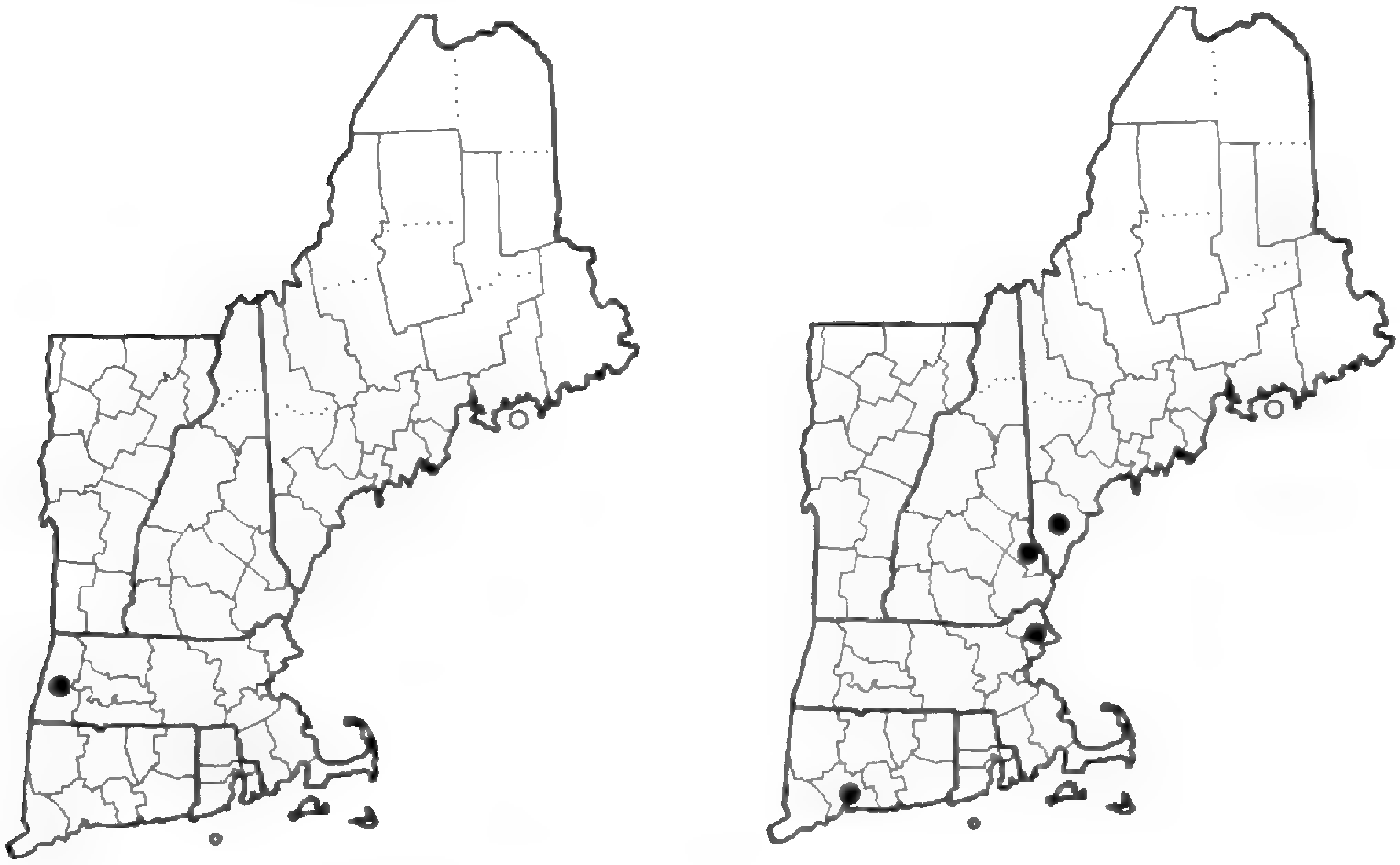
BROMUS JAPONICUS

Figure 17. Distribution maps for *BROMUS HORDEACEUS* subsp. *PSEUDOTHOMINEI, B. HORDEACEUS* subsp. *THOMINEI, B. INERMIS* and *B. JAPONICUS.*



Bromus kalmii

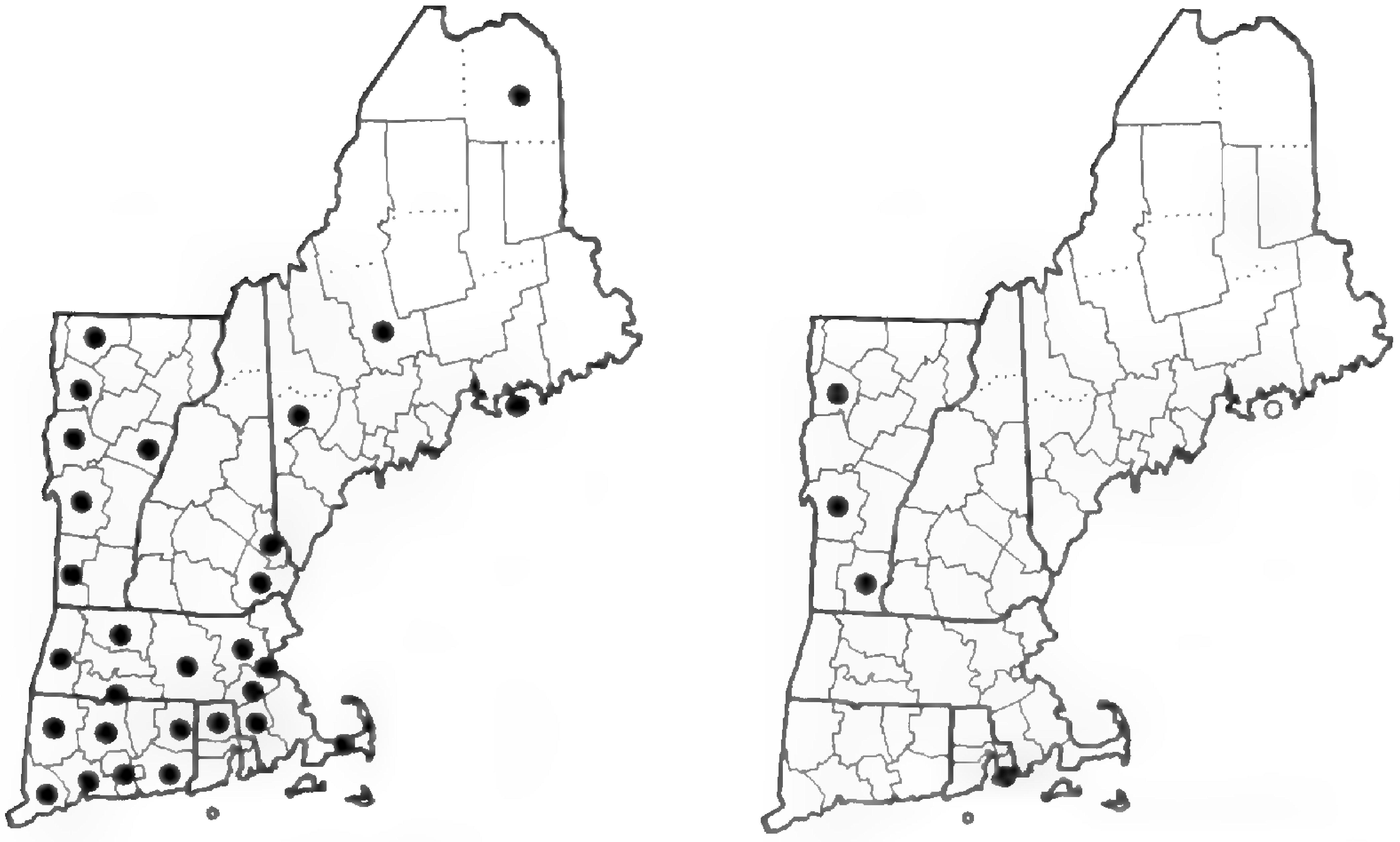
Bromus latiglumis



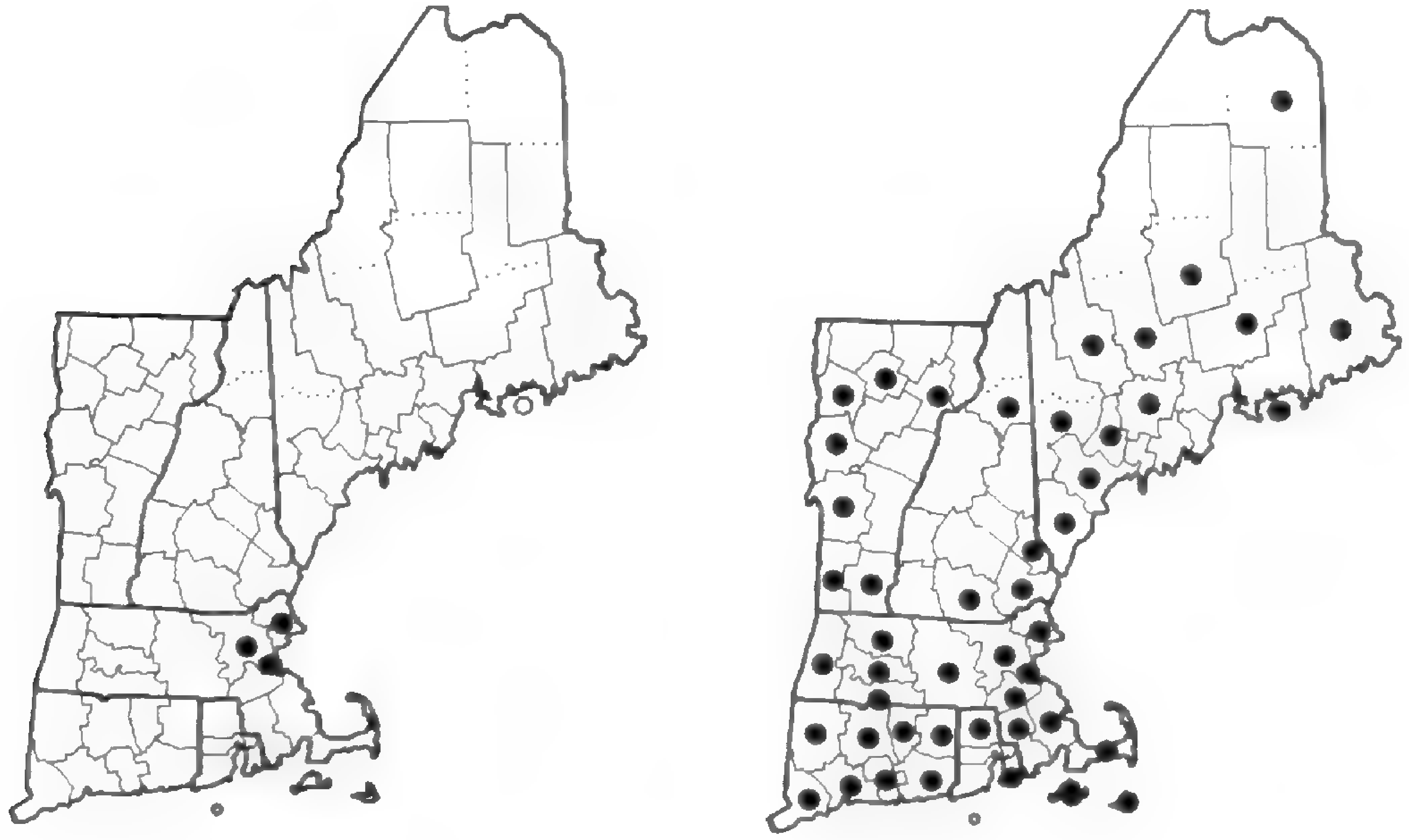
BROMUS LEPIDUS

BROMUS MARGINATUS

Figure 18. Distribution maps for *Bromus kalmii, B. latiglumis, B. LEPIDUS* and *B. MARGINATUS.*

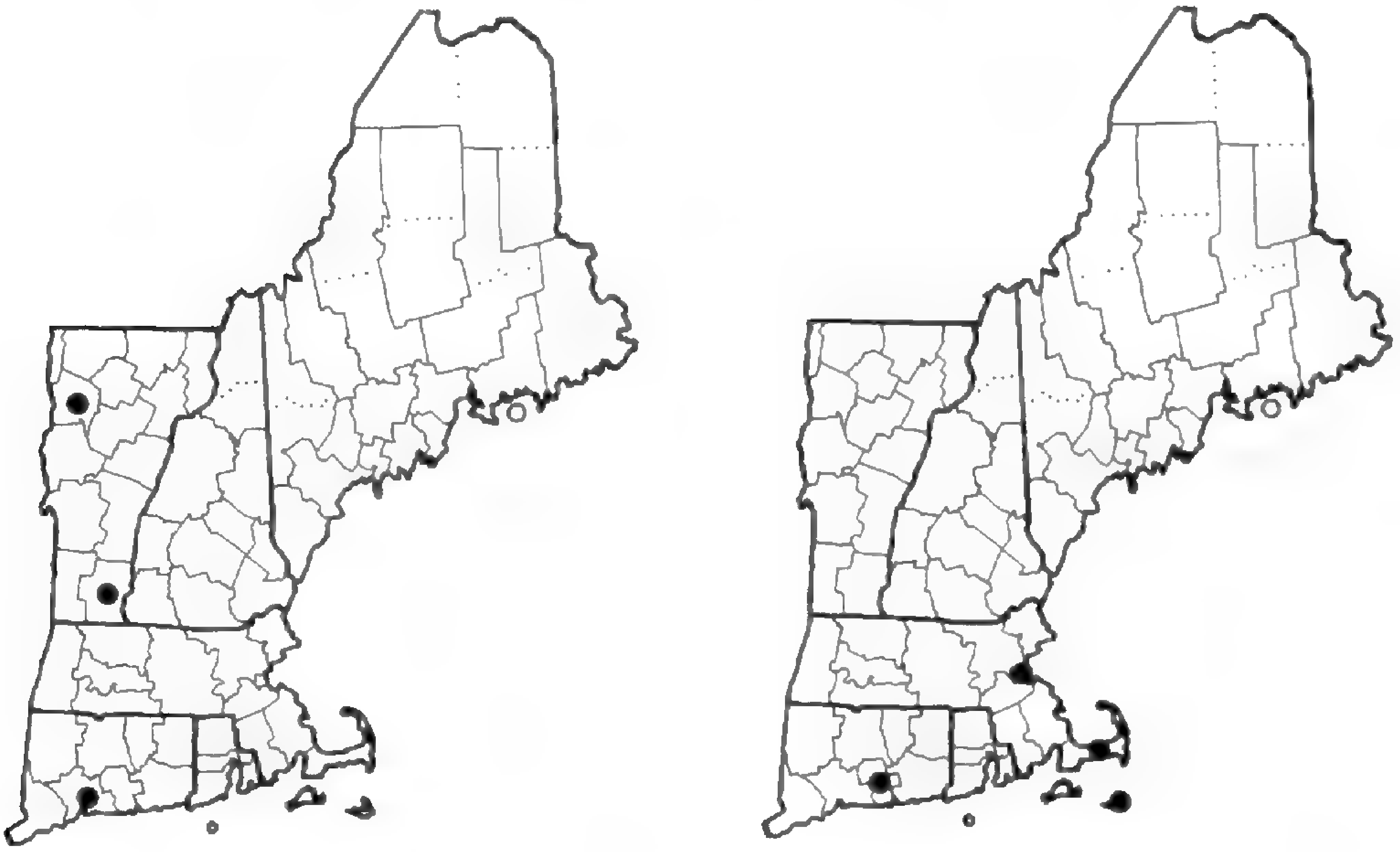


Bromus pubescens *BROMUS RACEMOSUS*



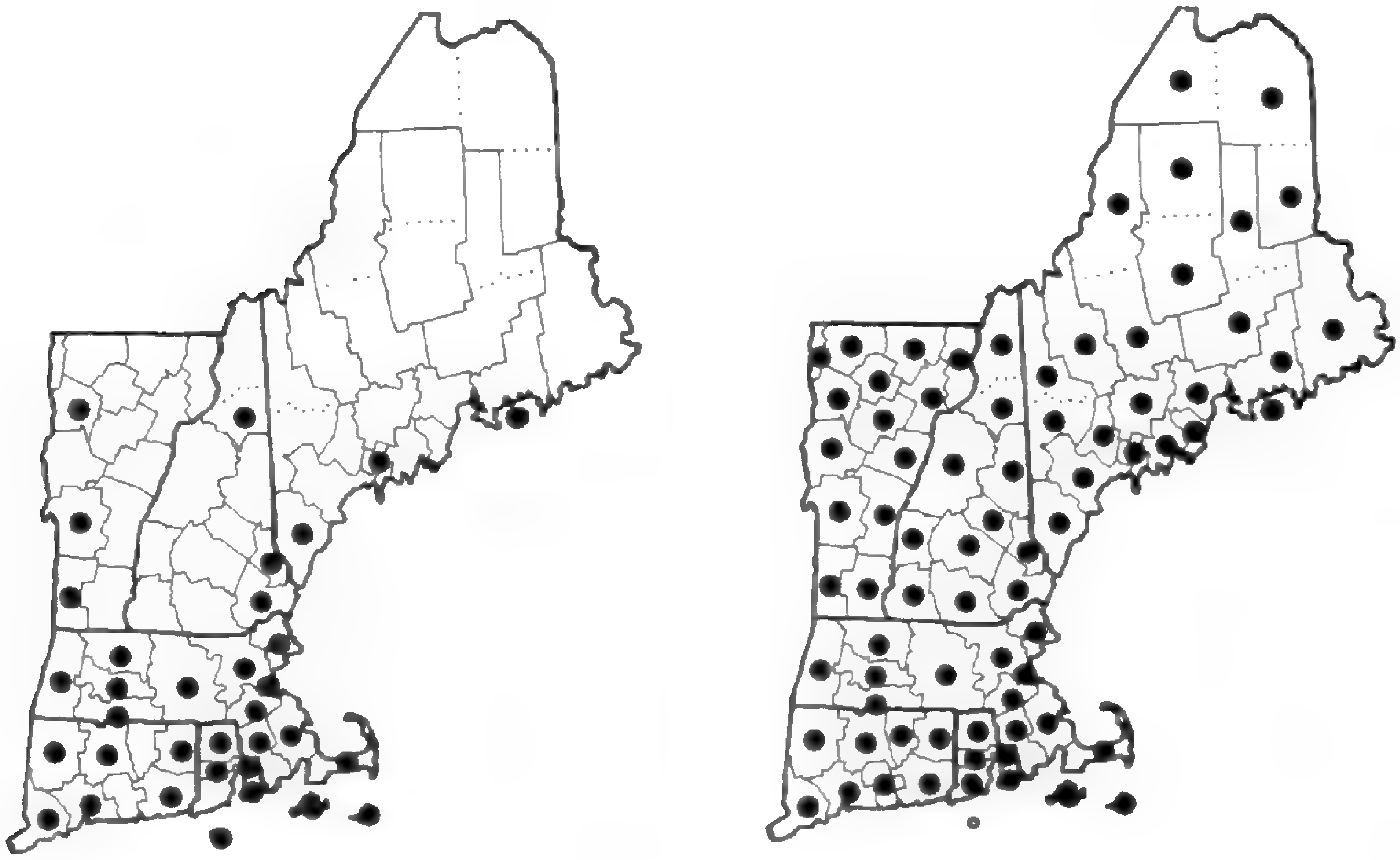
BROMUS RIGIDUS *BROMUS SECALINUS*

Figure 19. Distribution maps for *Bromus pubescens, B. RACEMOSUS, B. RIGIDUS* and *B. SECALINUS.*



BROMUS SQUARROSUS

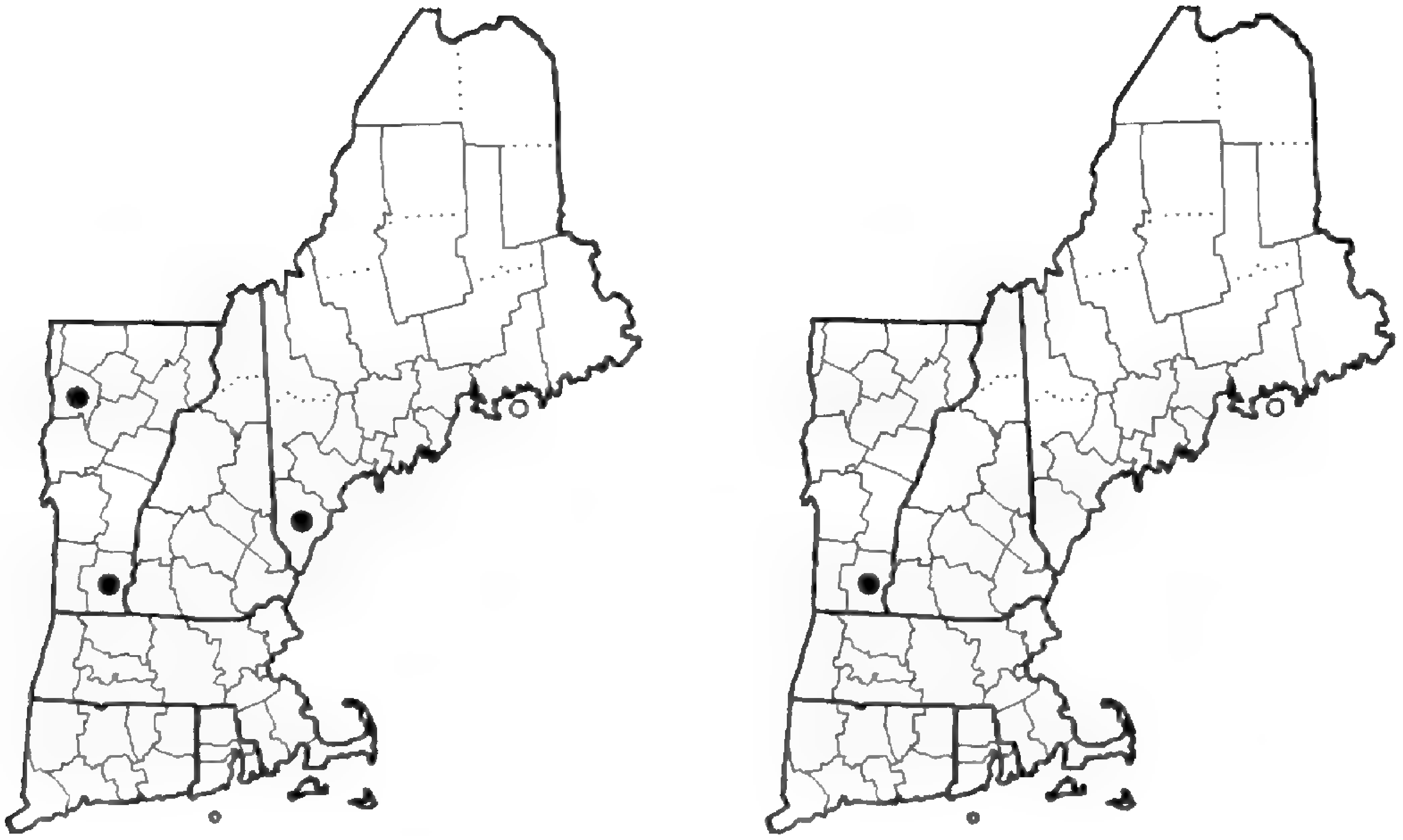
BROMUS STERILIS



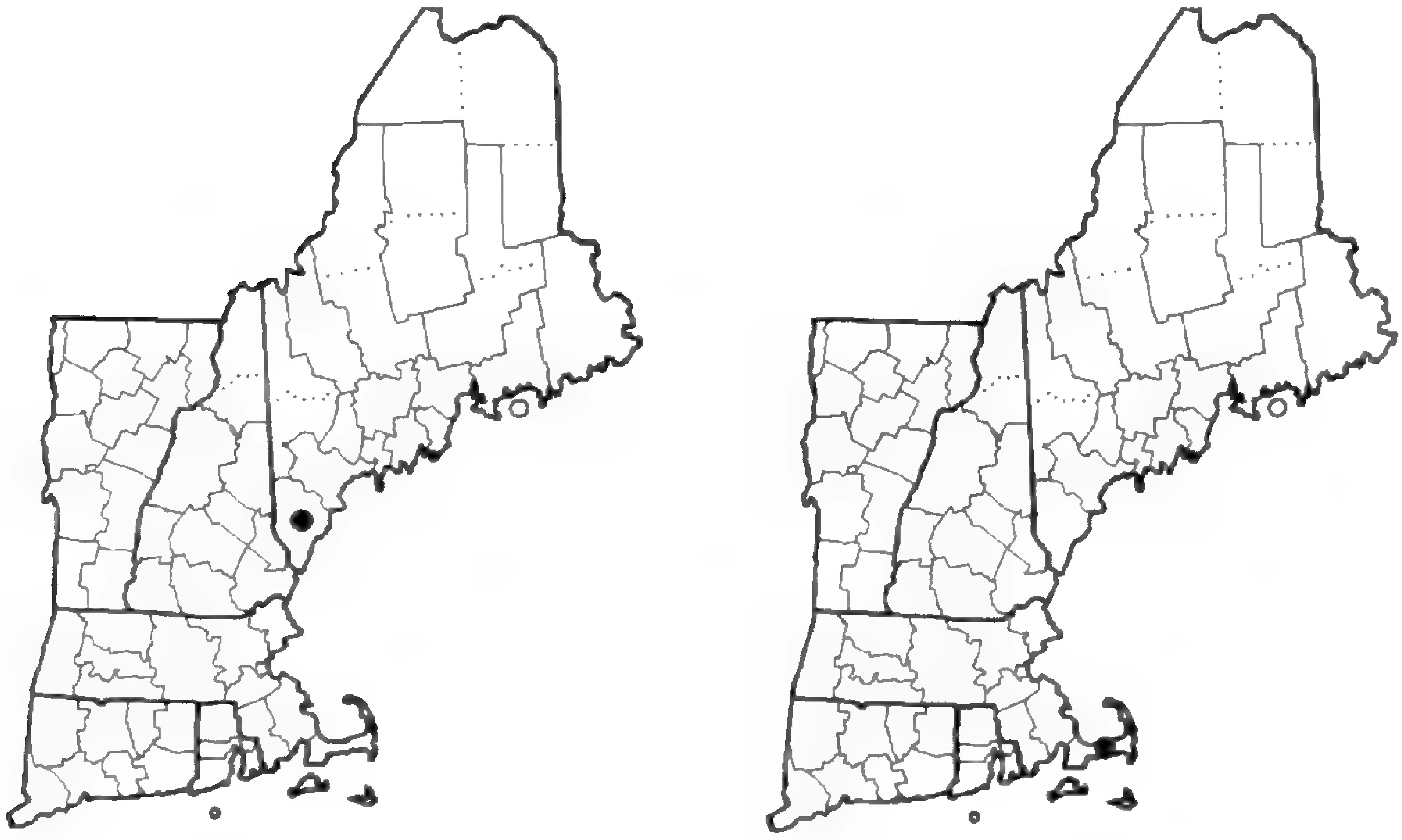
BROMUS TECTORUM

Calamagrostis canadensis
var. *canadensis*

Figure 20. Distribution maps for *BROMUS SQUARROSUS*, *B. STERILIS*, *B. TECTORUM* and *Calamagrostis canadensis* var. *canadensis*.

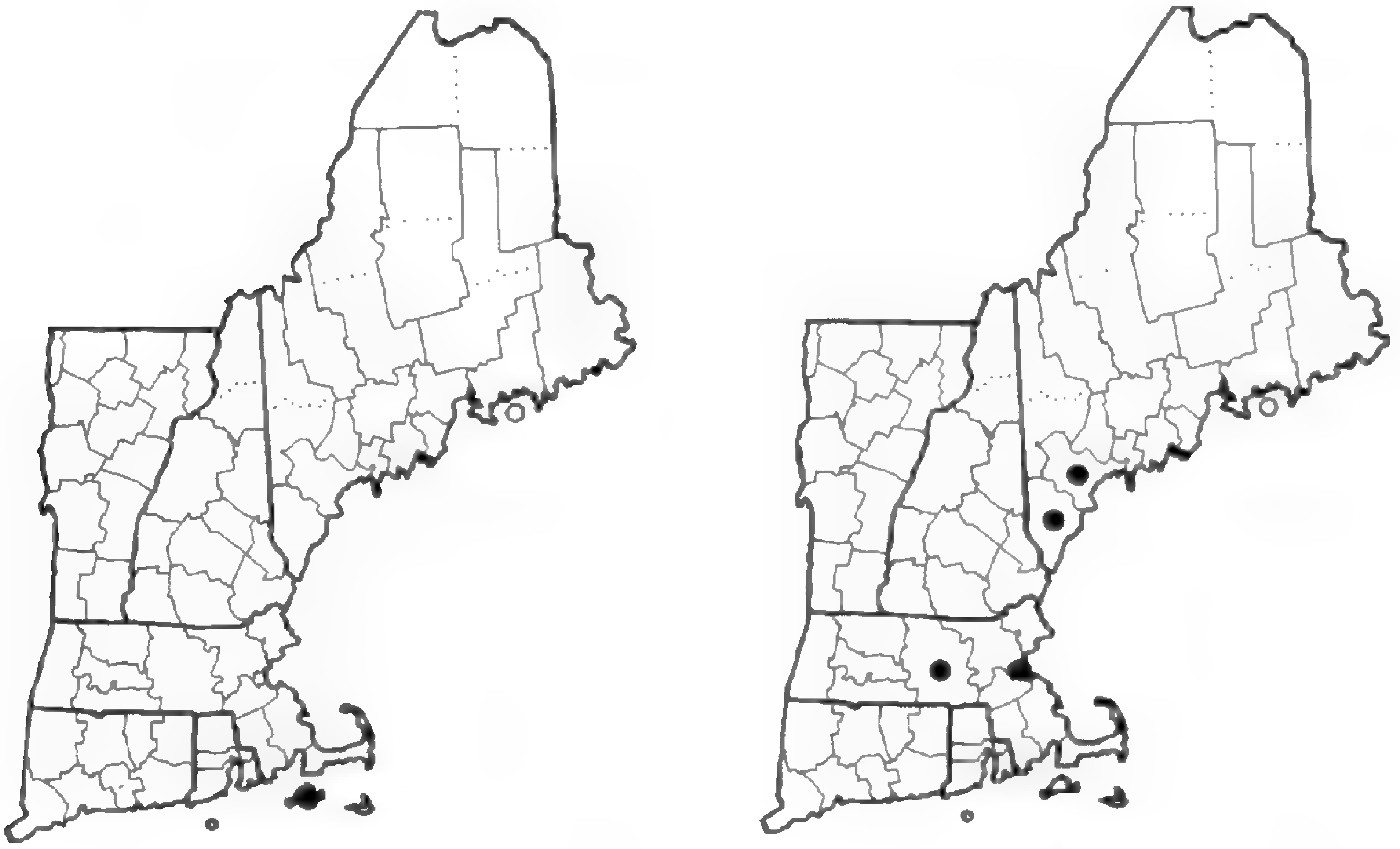


CENCHRUS SPINIFEX *CENCHRUS TRIBULOIDES*

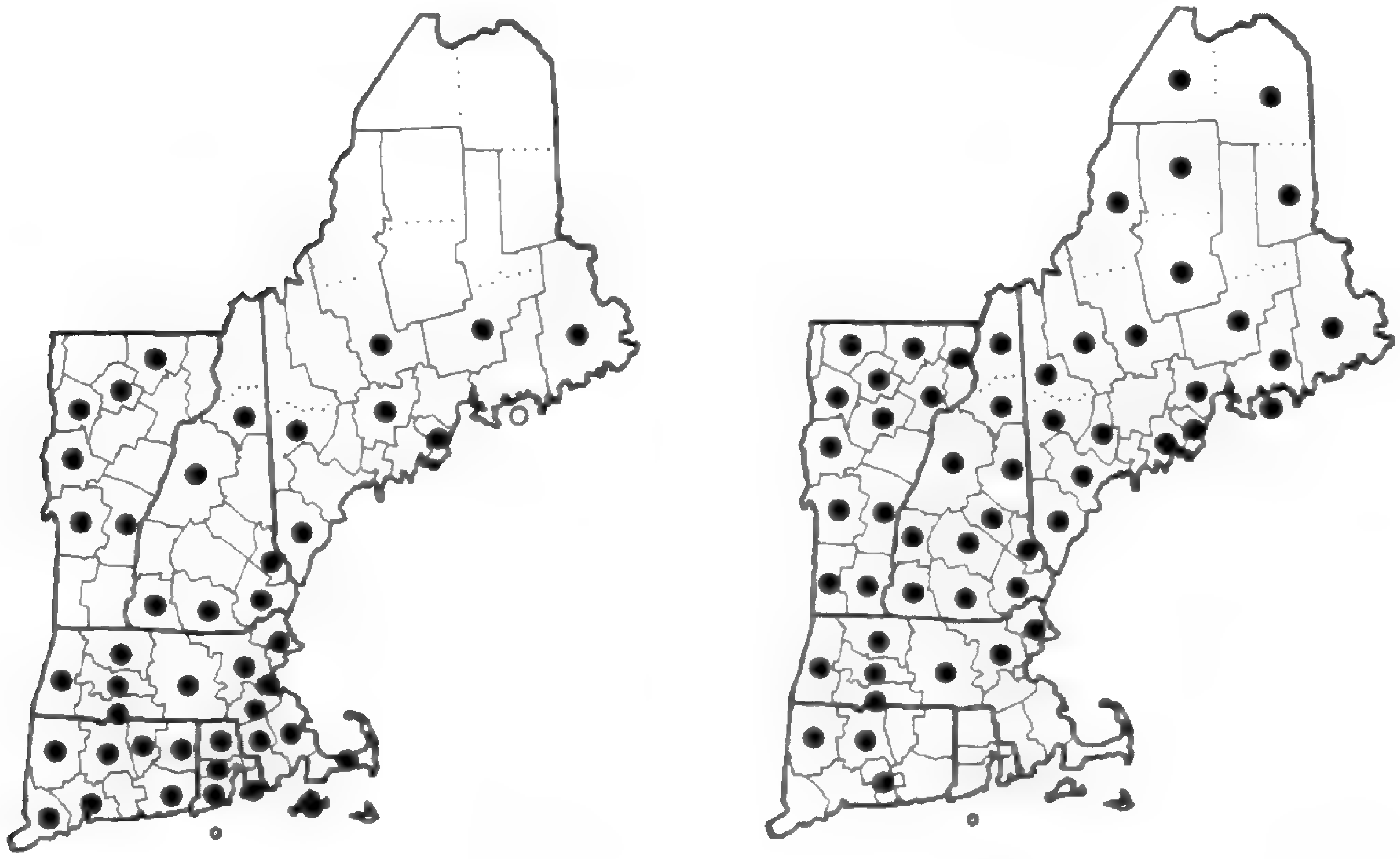


CHLORIS CUCULLATA *CHLORIS GAYANA*

Figure 23. Distribution maps for *CENCHRUS SPINIFEX, C. TRIBULOIDES, CHLORIS CUCULLATA* and *C. GAYANA.*

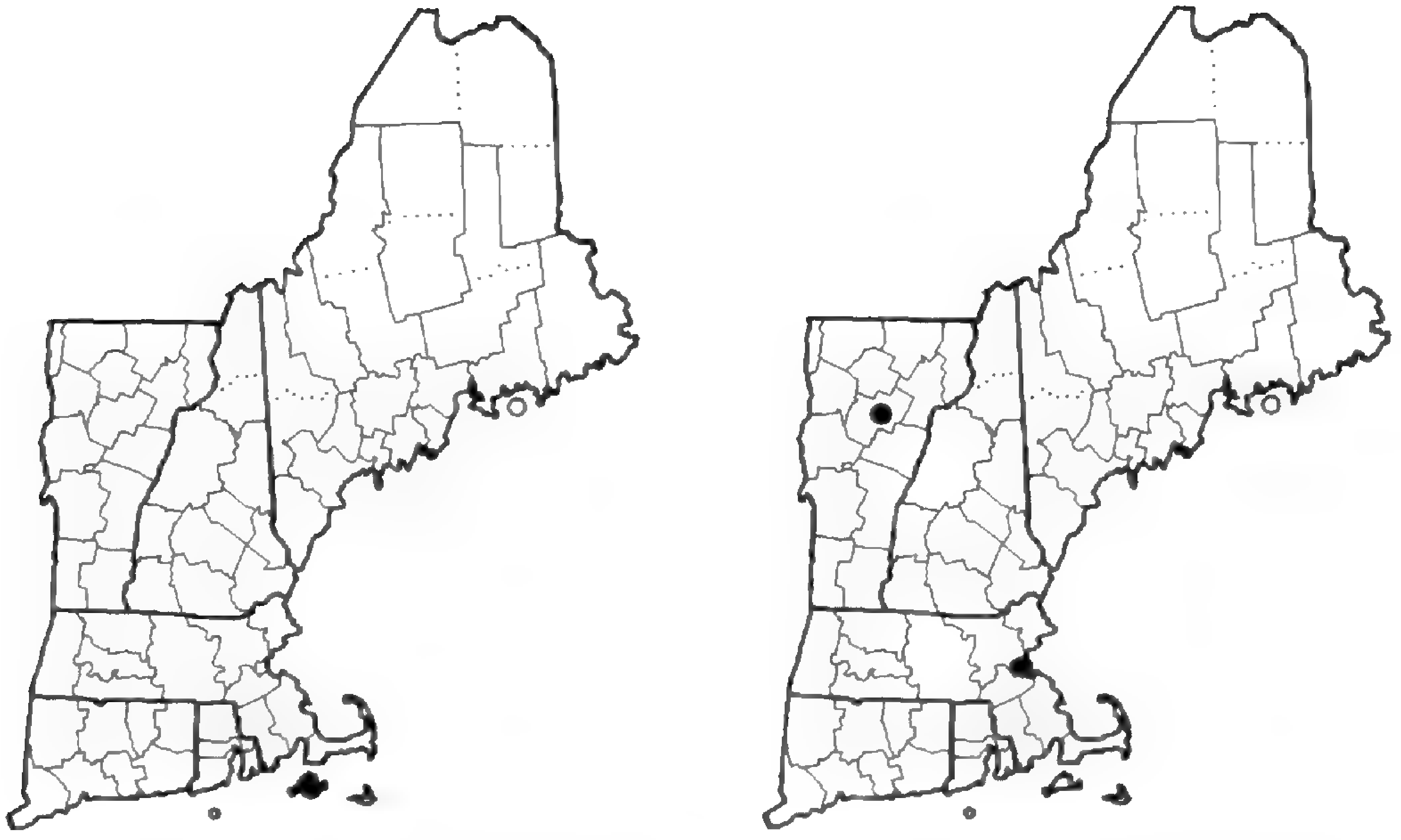


CHLORIS VERTICILLATA *CHLORIS VIRGATA*

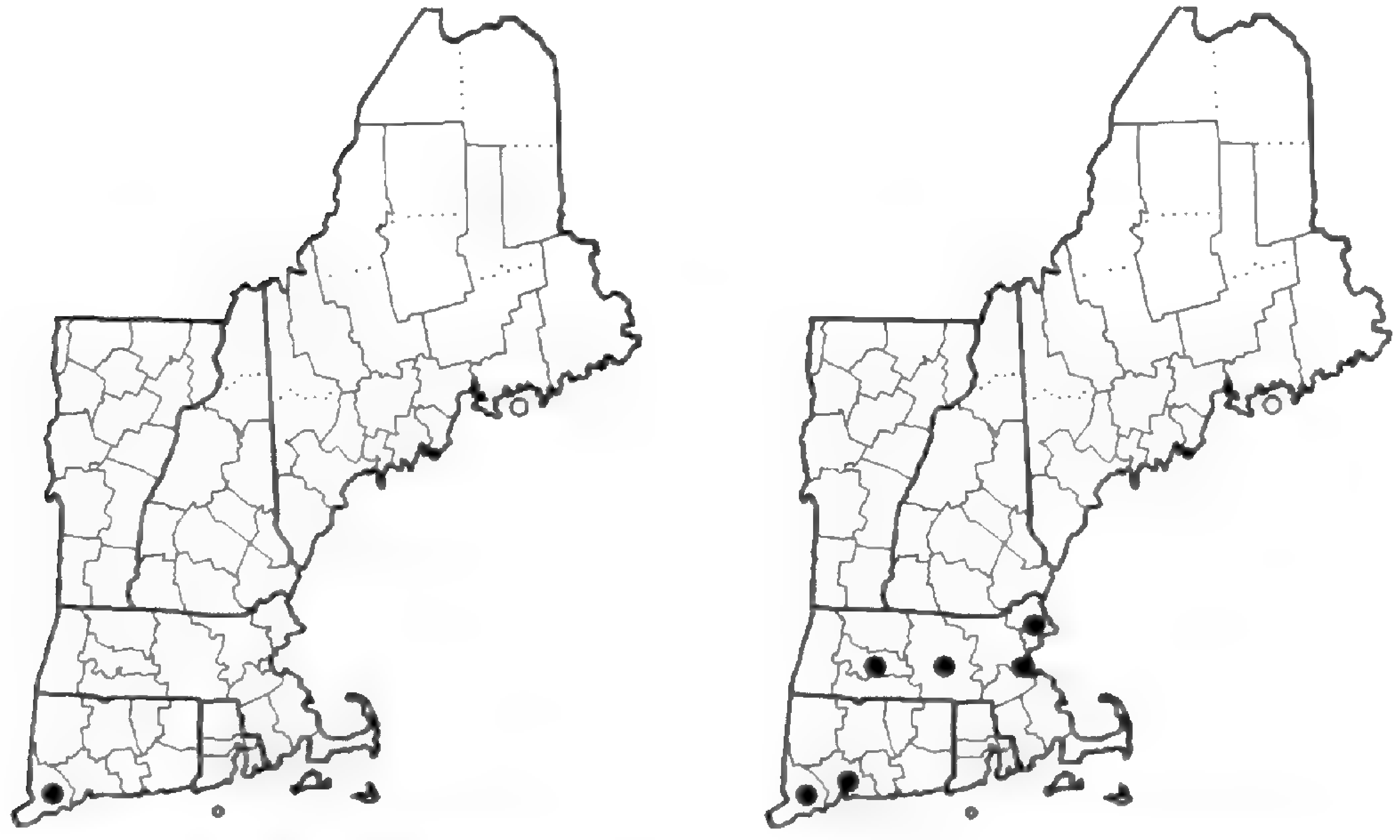


Cinna arundinacea *Cinna latifolia*

Figure 24. Distribution maps for *CHLORIS VERTICILLATA*, *C. VIRGATA*, *Cinna arundinacea* and *C. latifolia*.

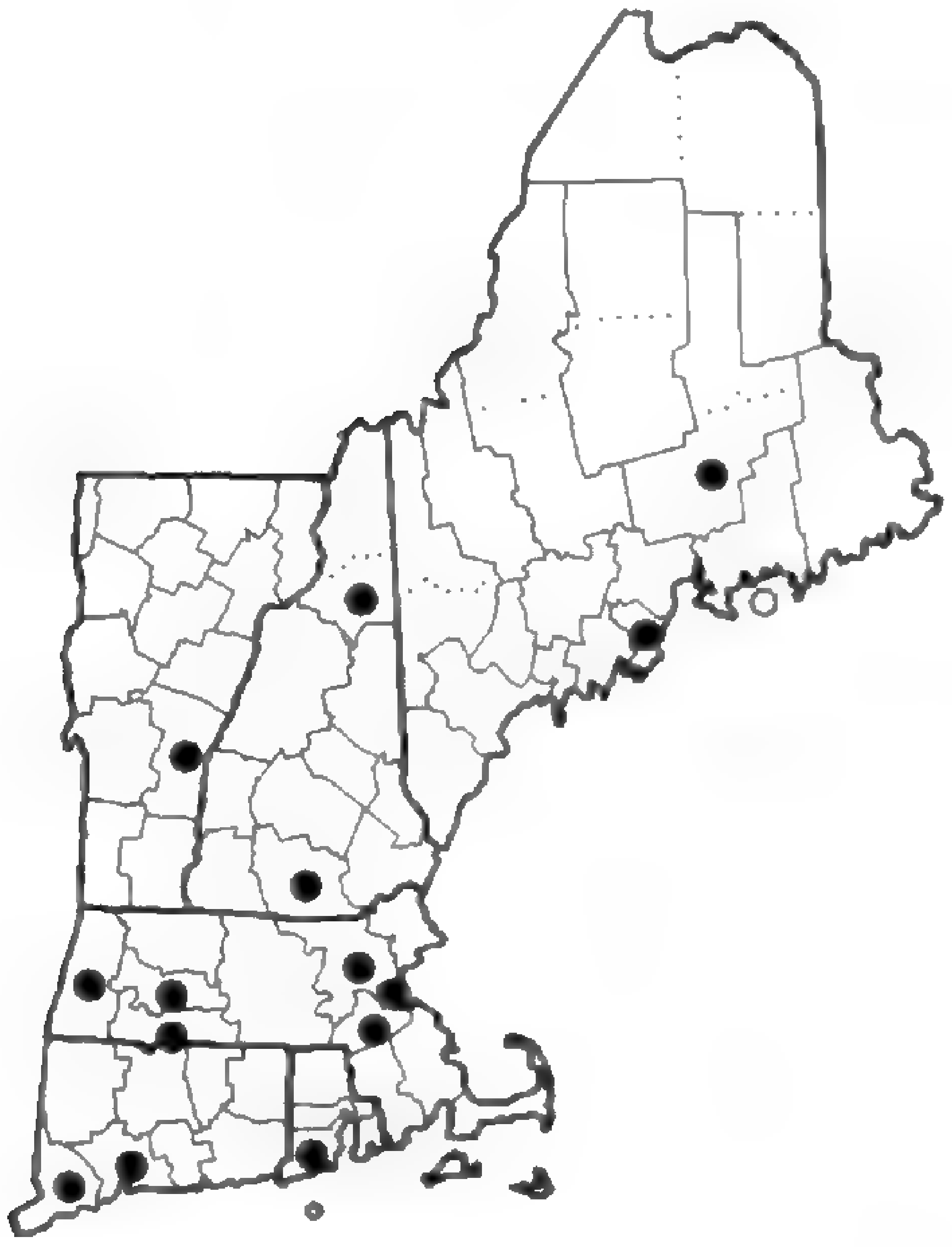


CORYNEPHORUS CANESCENS *CRYPSIS SCHOENOIDES*

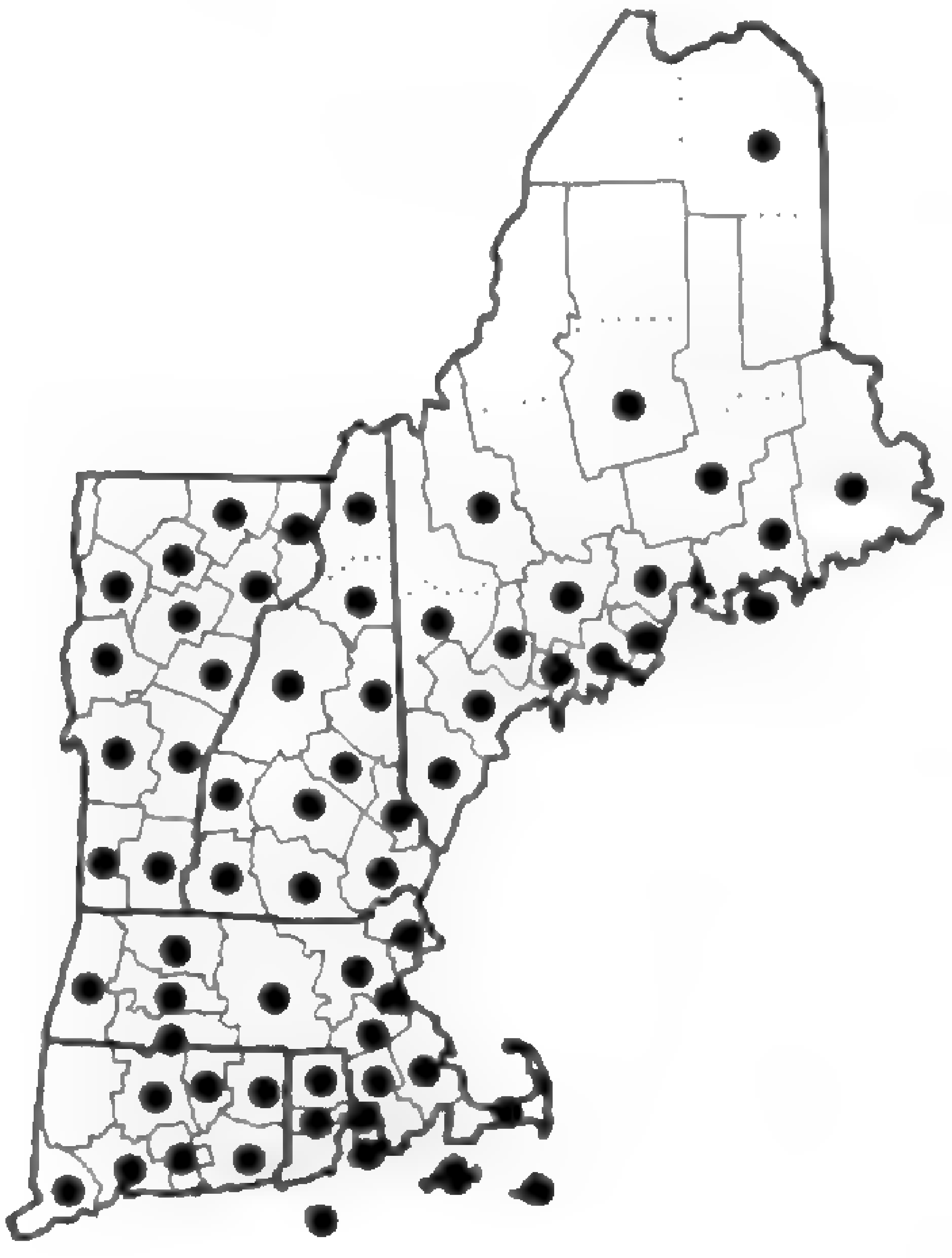


CYNODON ARISTIGLUMIS *CYNODON DACTYLON*

Figure 25. Distribution maps for *CORYNEPHORUS CANESCENS, CRYPSIS SCHOENOIDES, CYNODON ARISTIGLUMIS* and *C. DACTYLON*.

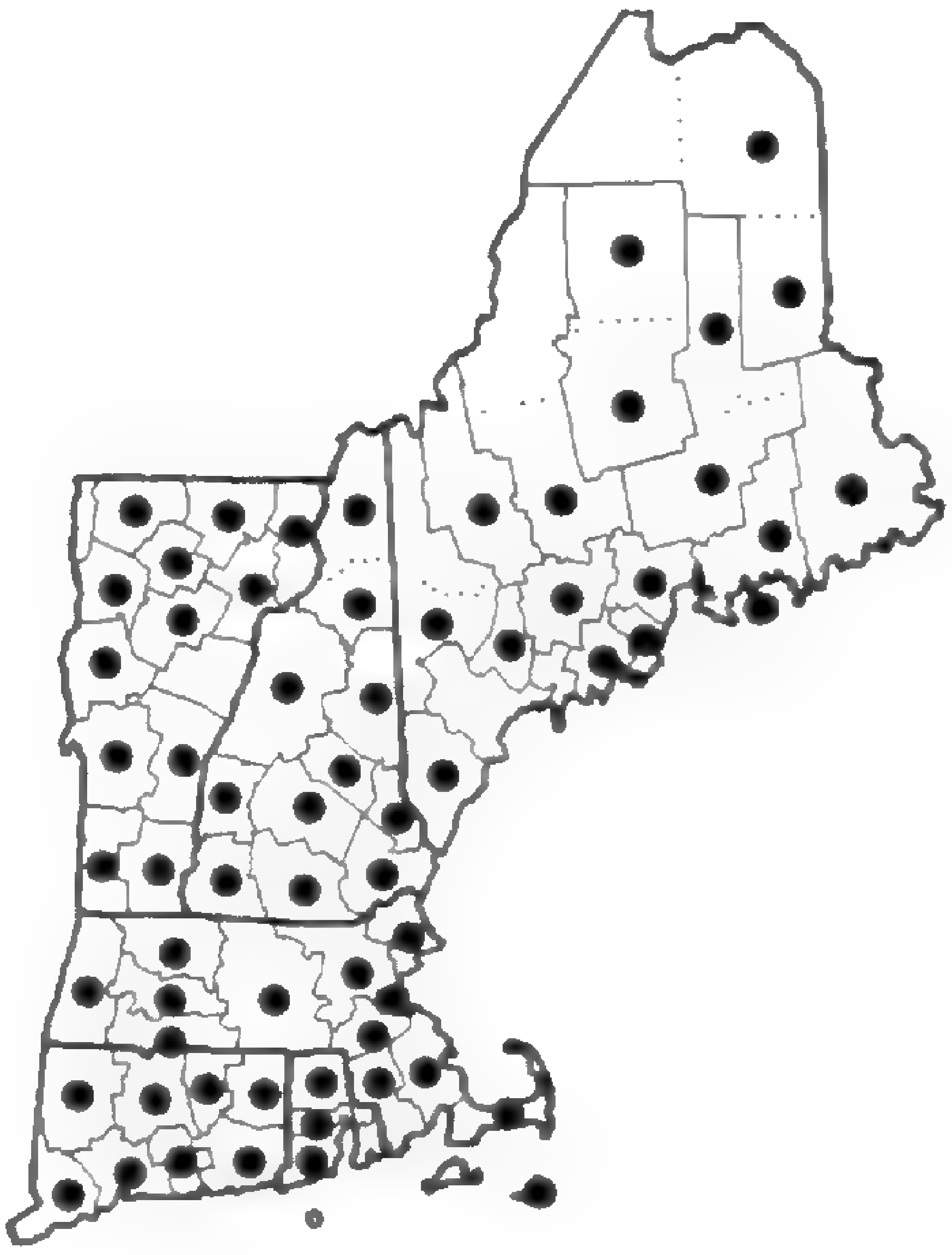


CYNOSURUS CRISTATUS



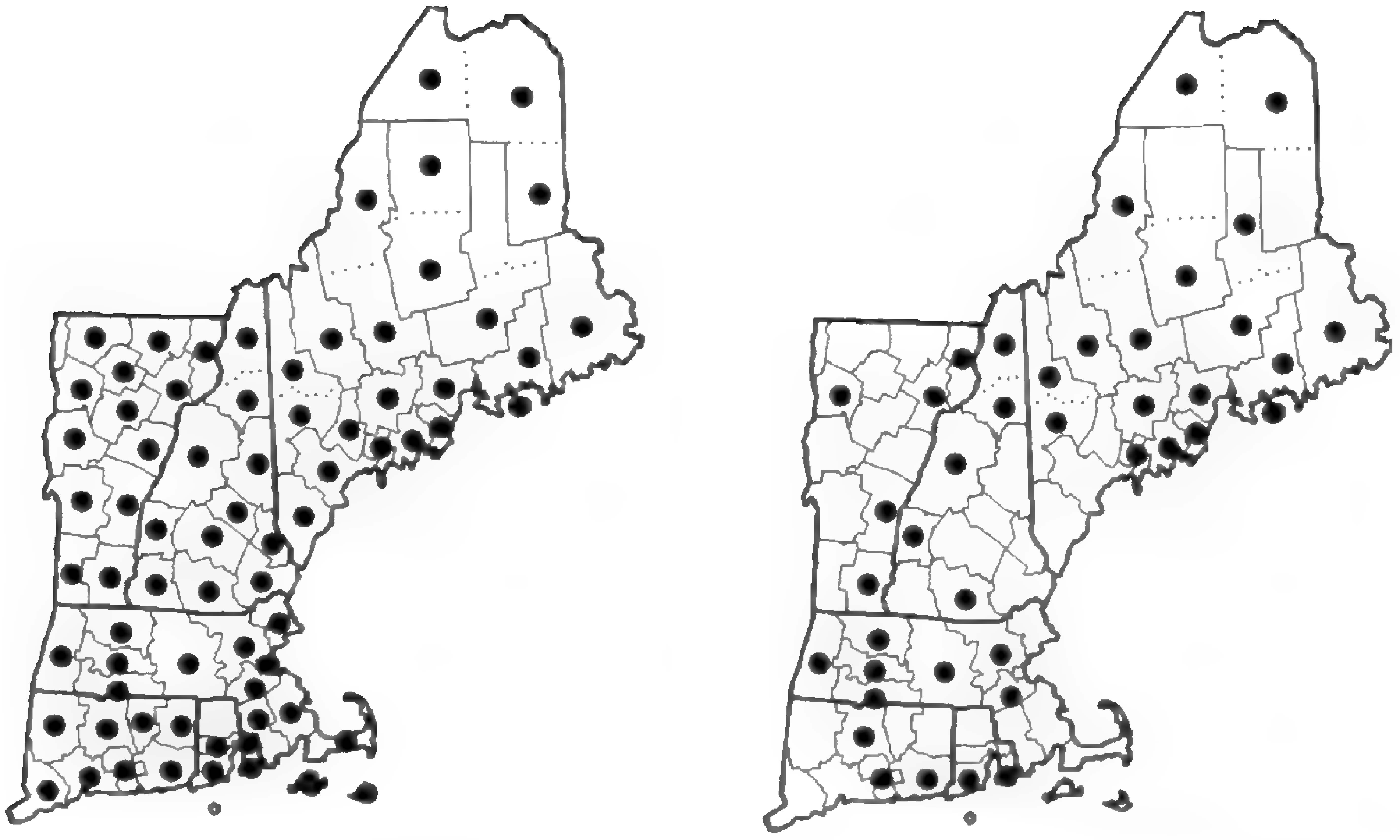
DACTYLIS GLOMERATA

DACTYLOCTENIUM AEGYPTIUM



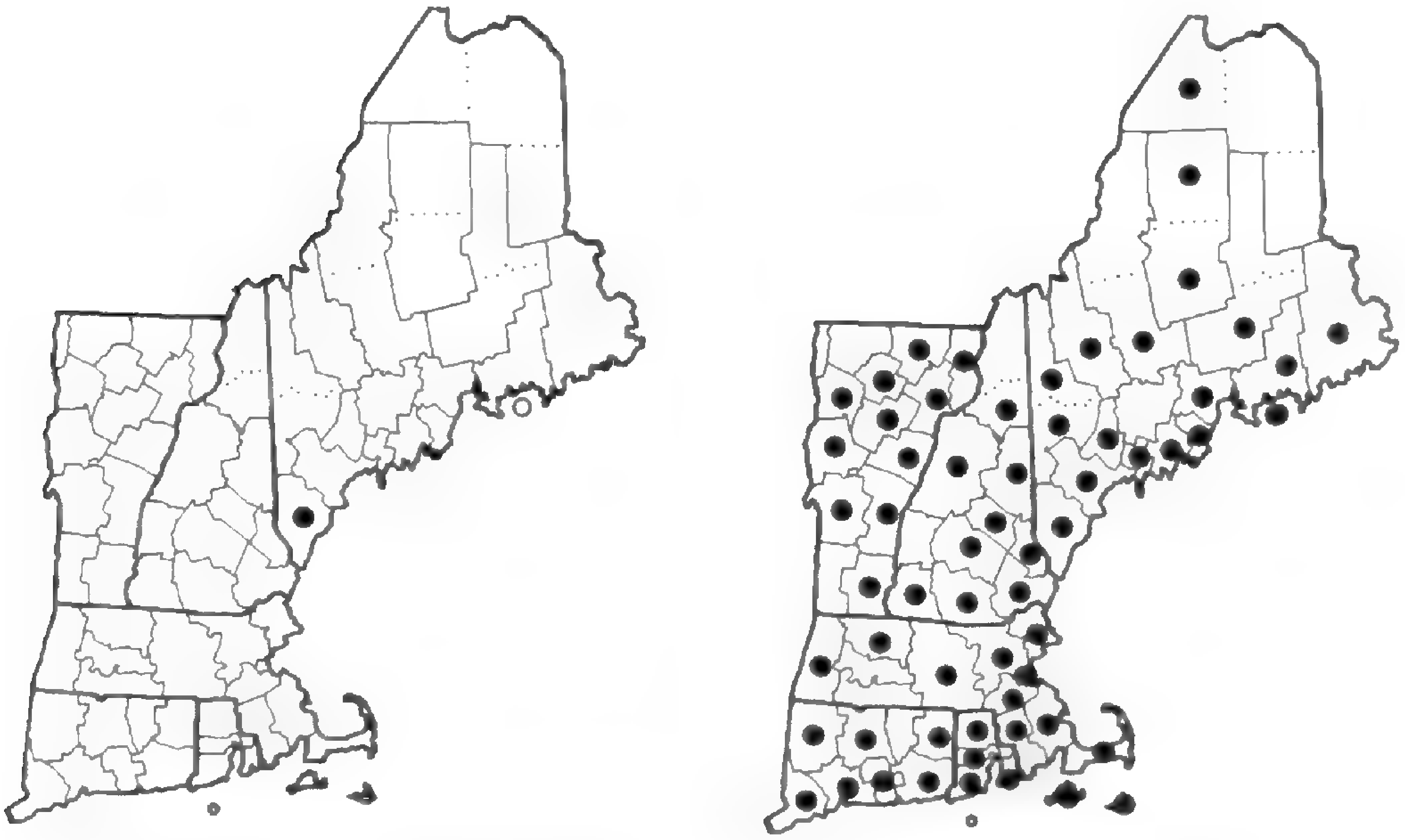
Danthonia compressa

Figure 26. Distribution maps for *CYNOSURUS CRISTATUS, DACTYLIS GLOMERATA, DACTYLOCTENIUM AEGYPTIUM* and *Danthonia compressa.*



Danthonia spicata

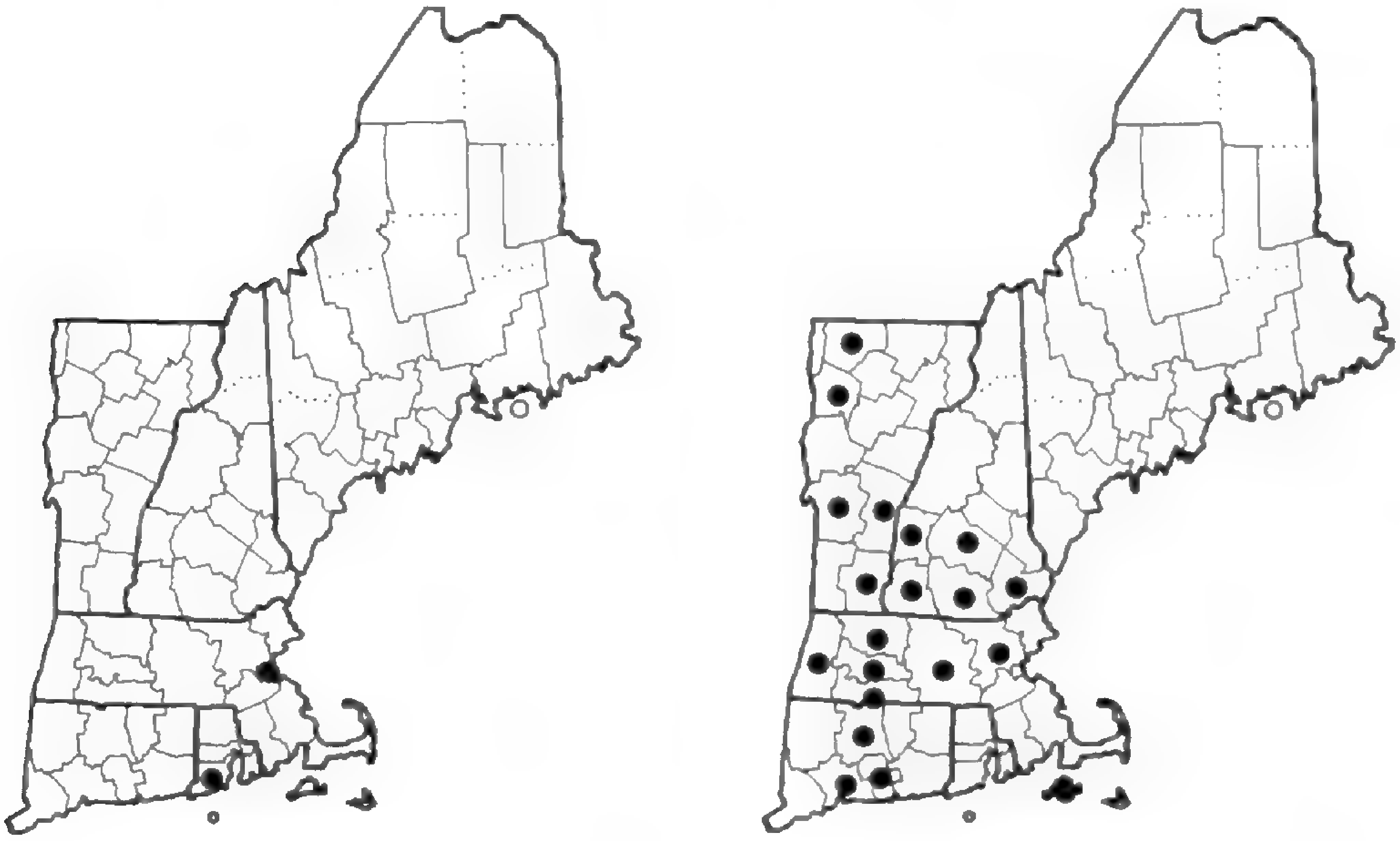
Deschampsia cespitosa



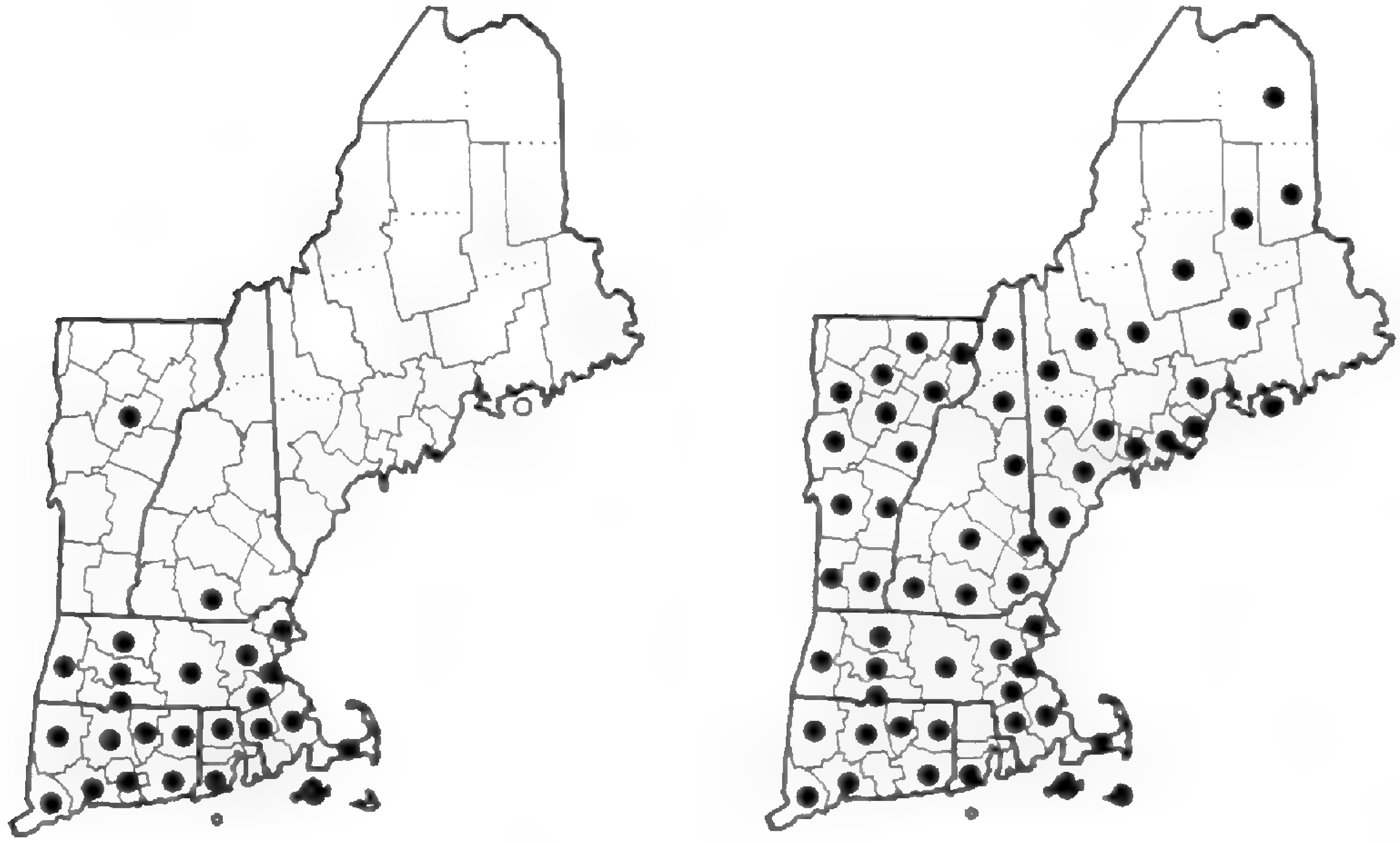
DESCHAMPSIA DANTHONIOIDES

Deschampsia flexuosa

Figure 27. Distribution maps for *Danthonia spicata, Deschampsia cespitosa, D. DANTHONIOIDES* and *D. flexuosa.*

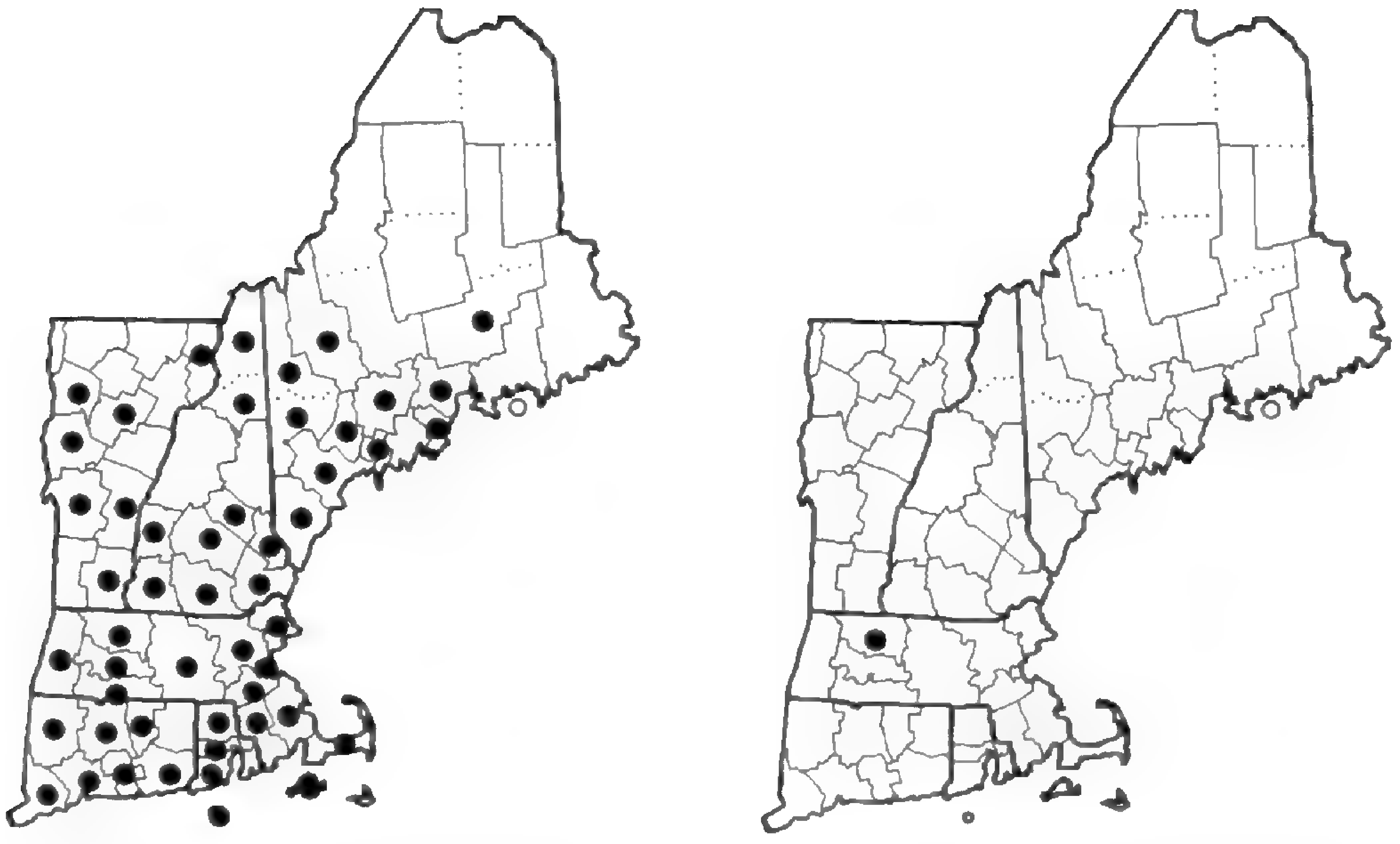


DESMAZERIA RIGIDA *Digitaria cognata*



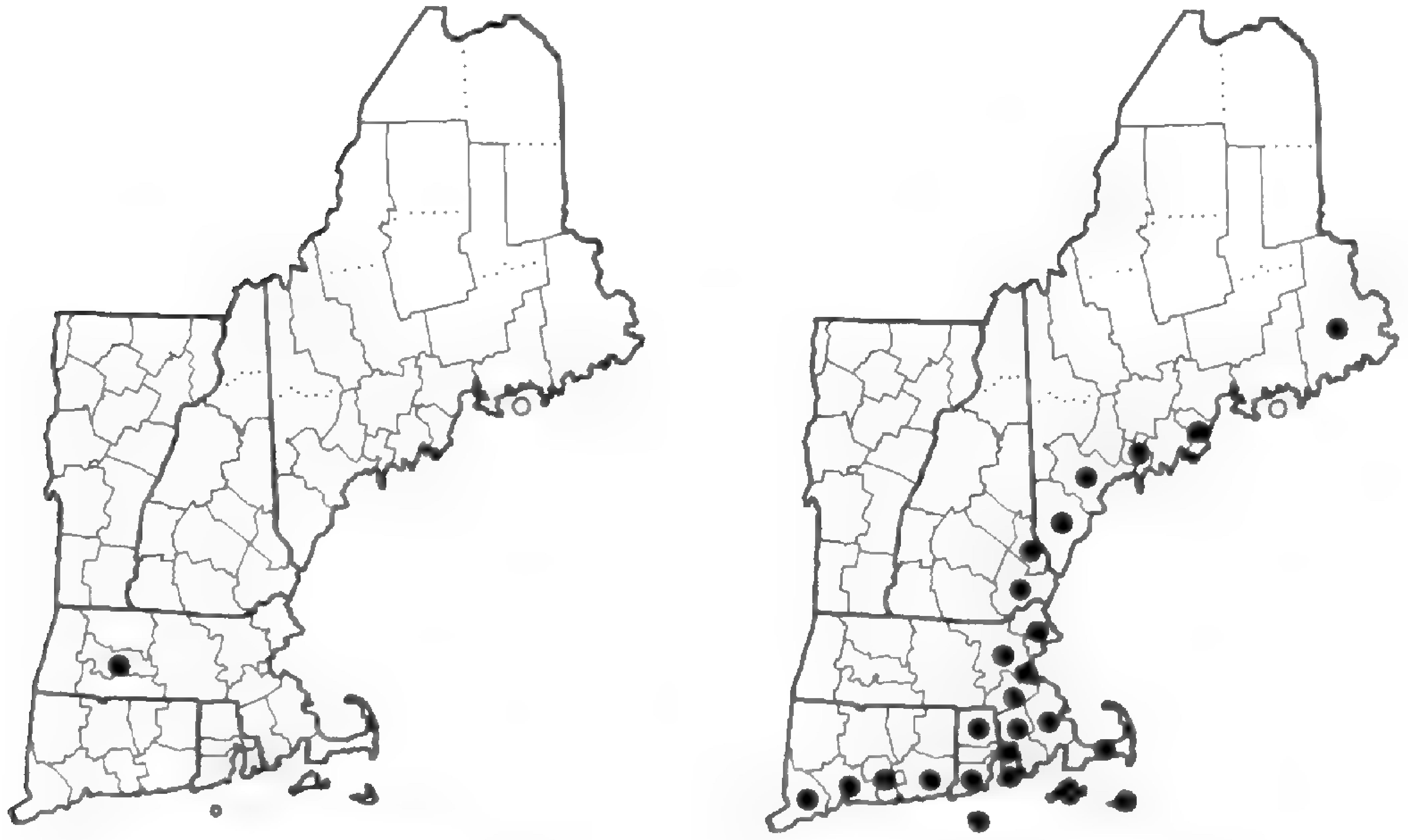
Digitaria filiformis *DIGITARIA ISCHAEMUM*

Figure 28. Distribution maps for *DESMAZERIA RIGIDA, Digitaria cognata, D. filiformis* and *D. ISCHAEMUM.*



DIGITARIA SANGUINALIS

DIGITARIA VIOLASCENS

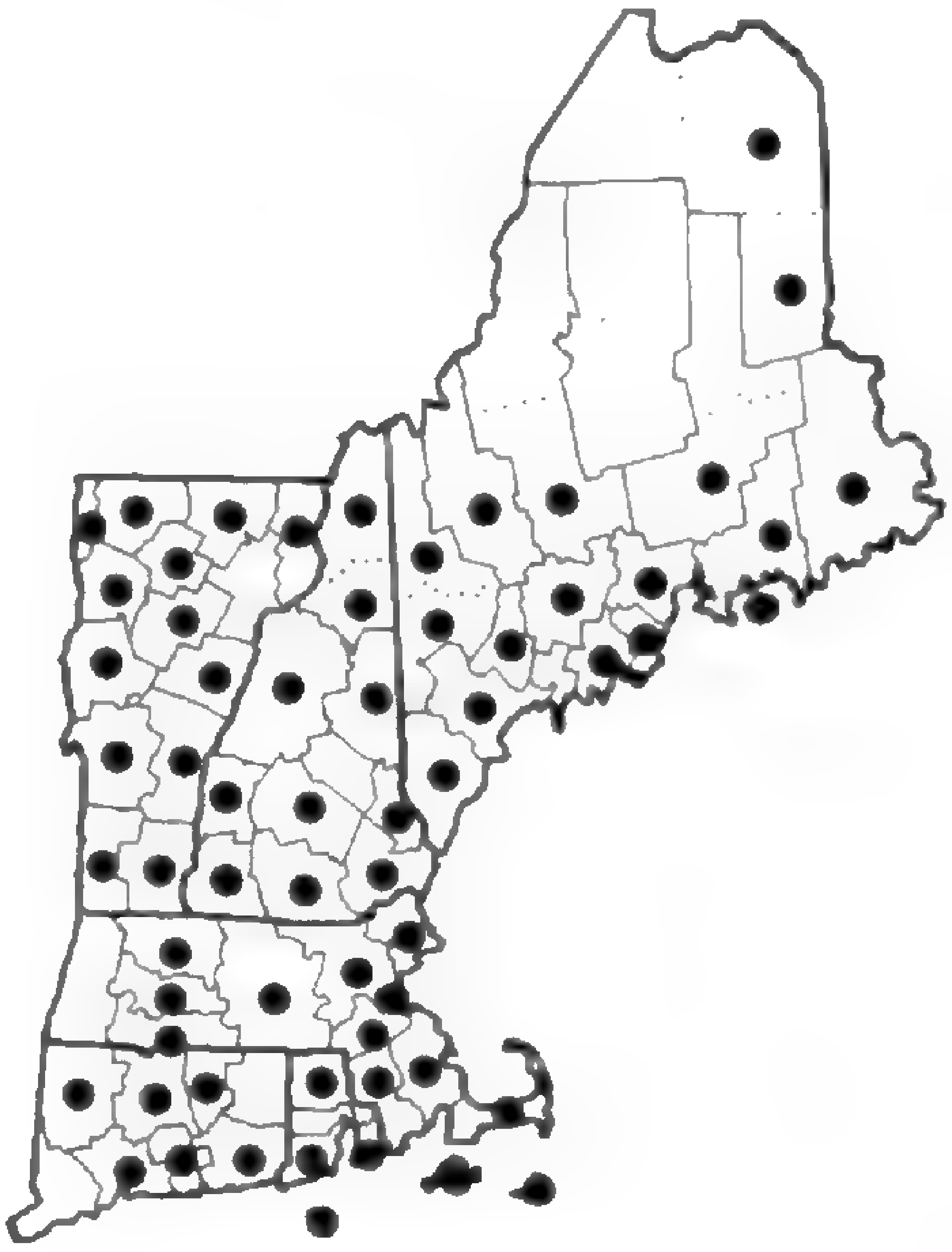


DIGITARIA ISCHAEMUM x
D. SANGUINALIS

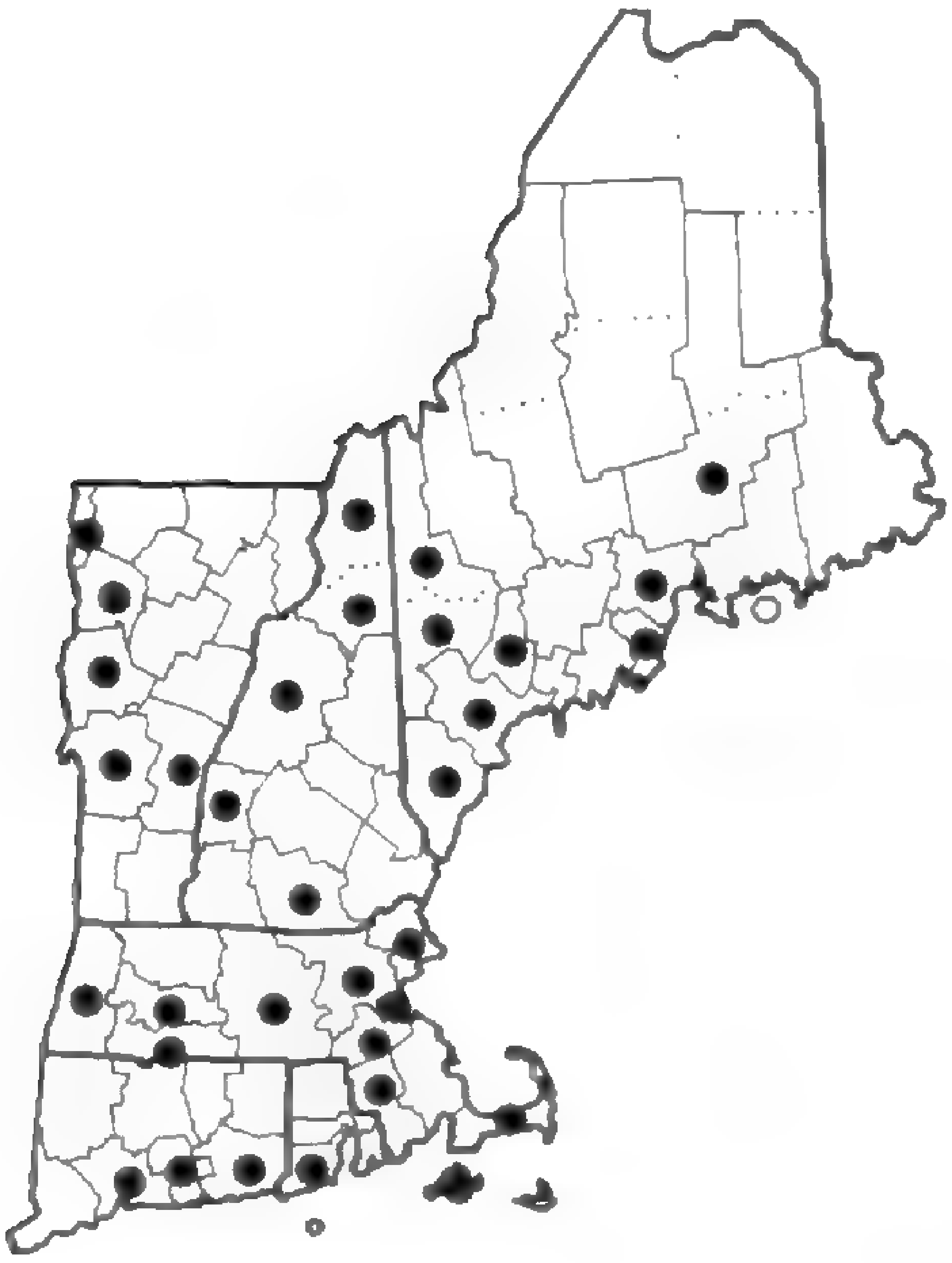
Distichlis spicata

Figure 29. Distribution maps for *DIGITARIA SANGUINALIS, D. VIOLASCENS, D. ISCHAEMUM* × *D. SANGUINALIS* and *Distichlis spicata.*

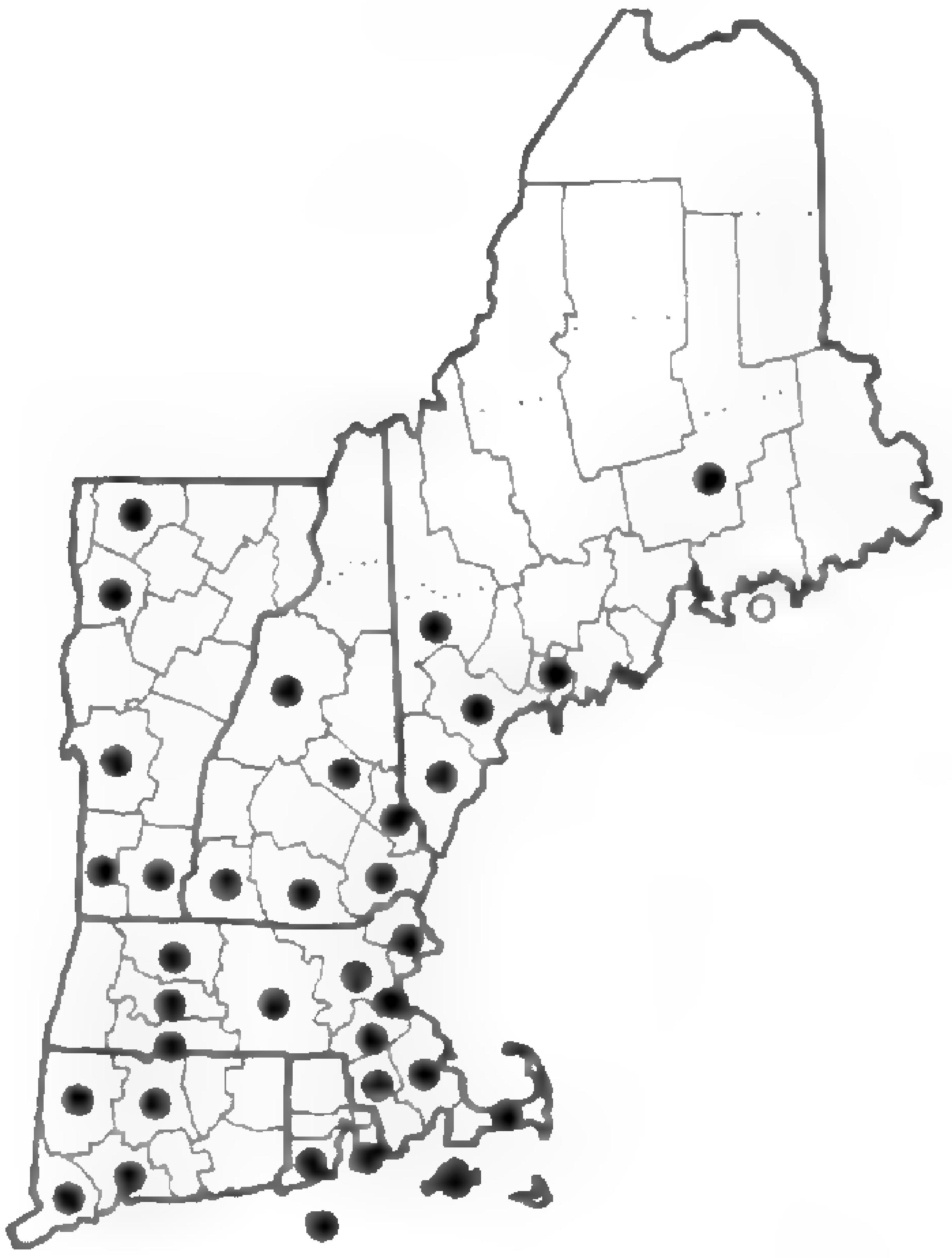
ECHINOCHLOA COLONA



ECHINOCHLOA CRUSGALLI

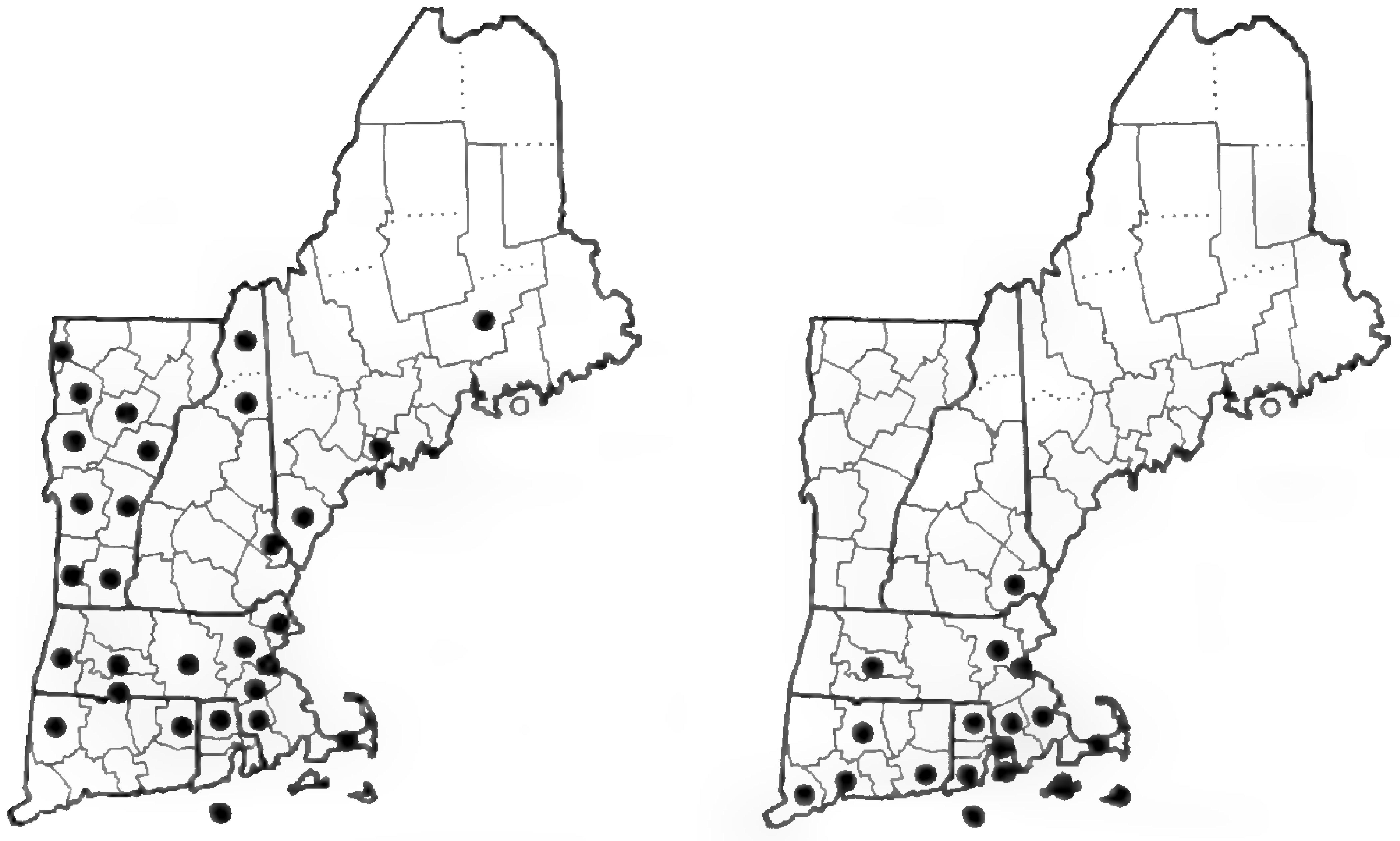


ECHINOCHLOA FRUMENTACEA



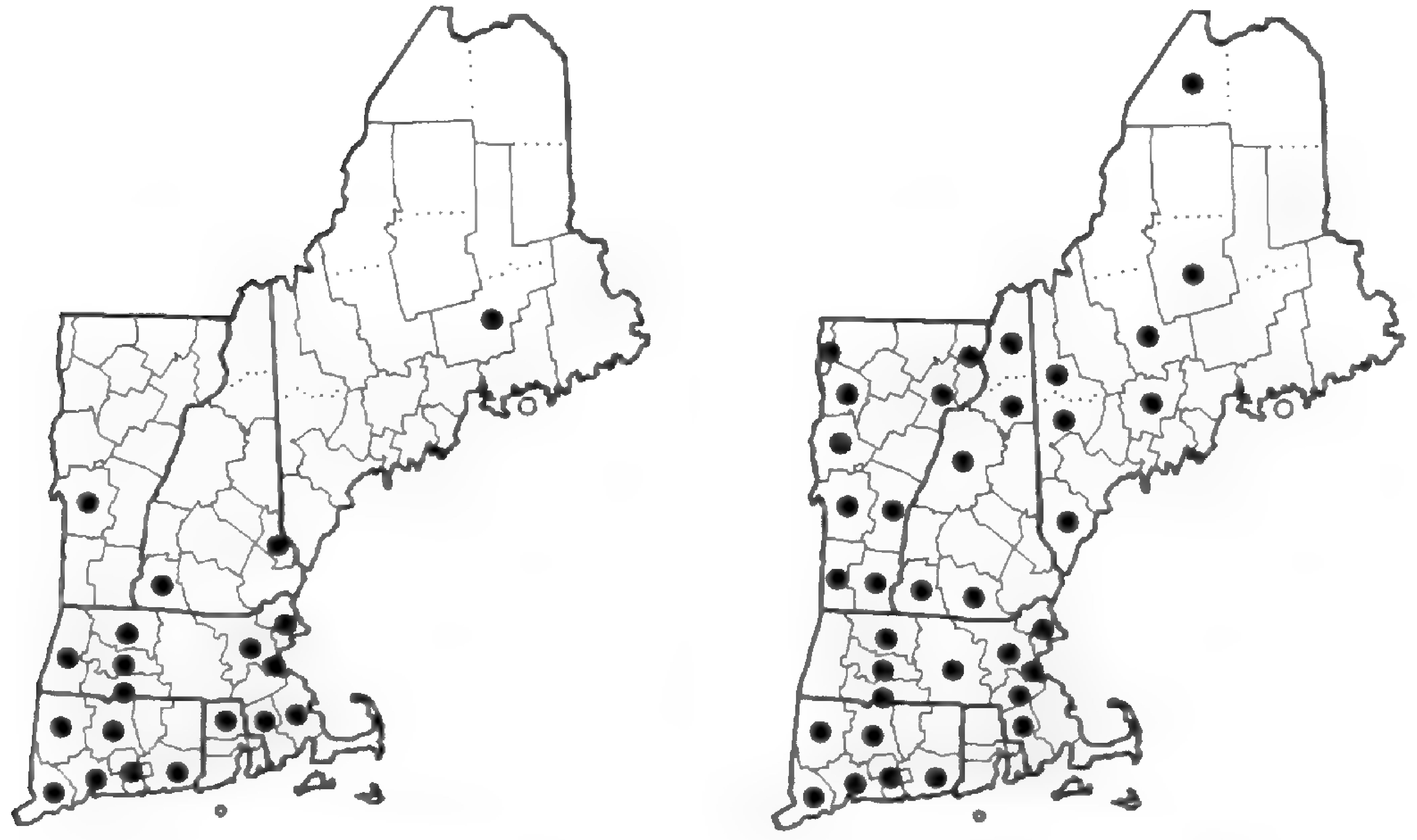
Echinochloa muricata
var. *muricata*

Figure 30. Distribution maps for *ECHINOCHLOA COLONA, E. CRUSGALLI, E. FRUMENTACEA* and *E. muricata* var. *muricata.*



Echinochloa muricata var. *microstachya*

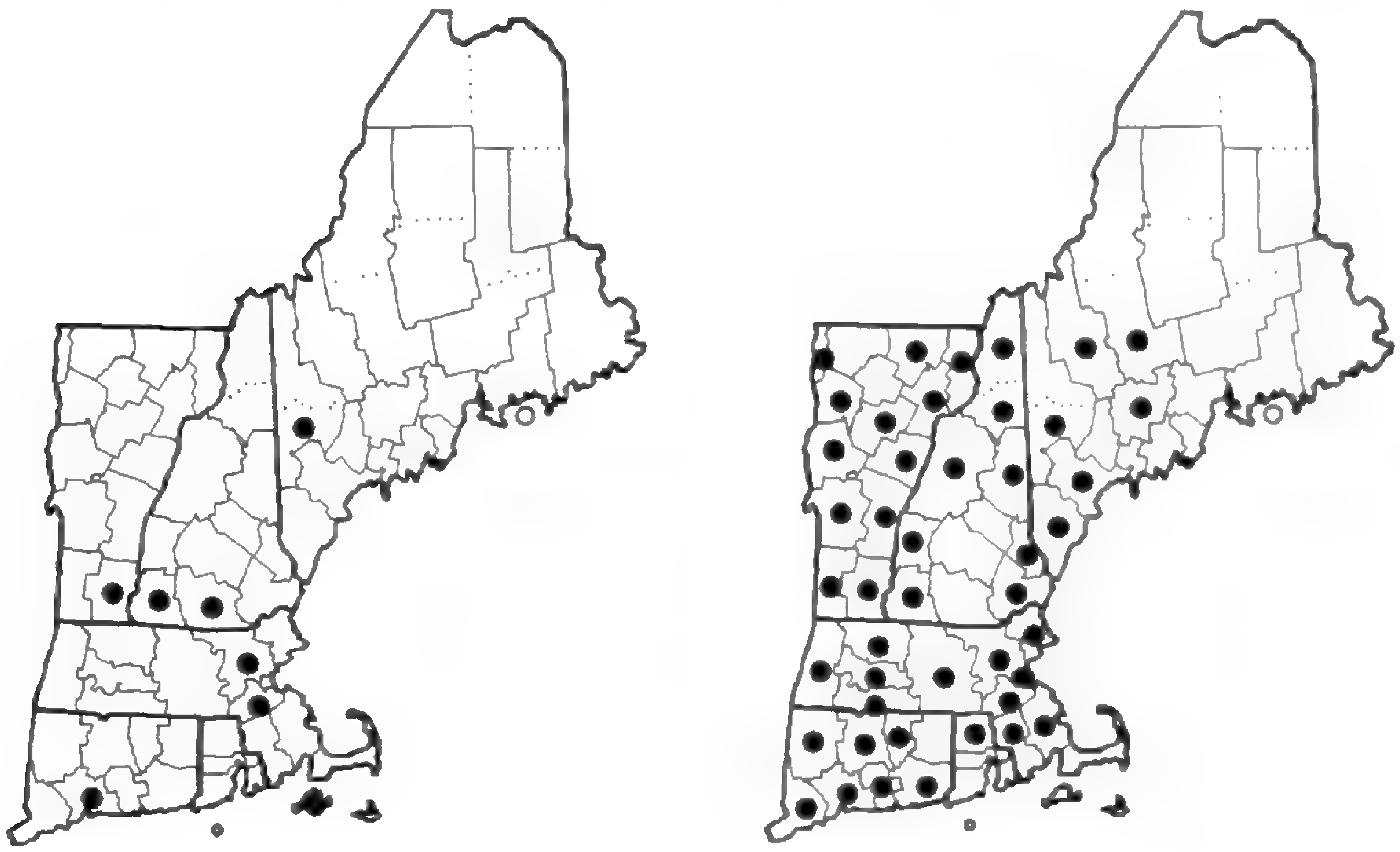
Echinochloa walteri



ELEUSINE INDICA

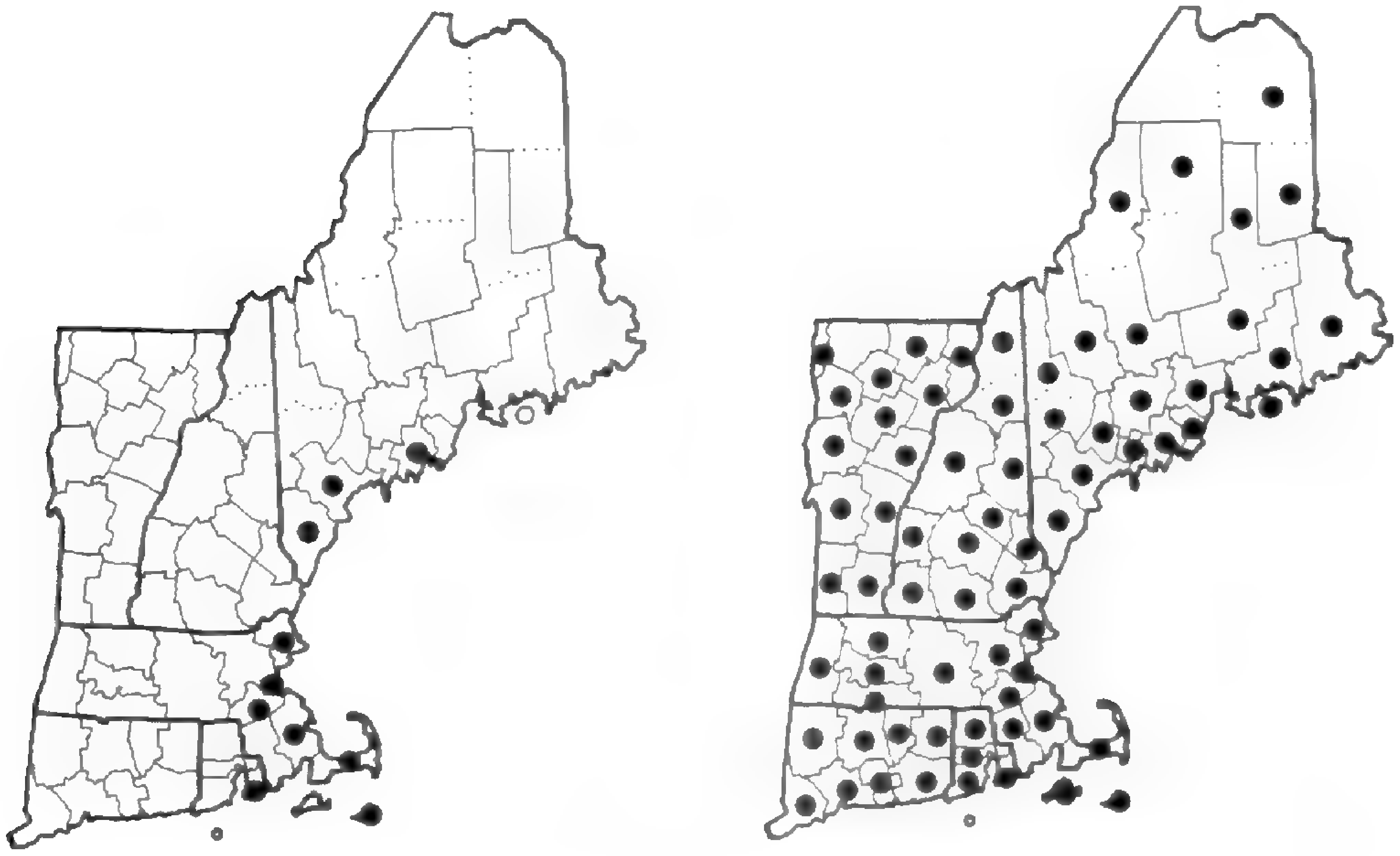
Elymus canadensis

Figure 31. Distribution maps for *Echinochloa muricata* var. *microstachya*, *E. walteri*, *ELEUSINE INDICA* and *Elymus canadensis*.



Elymus glabriflorus

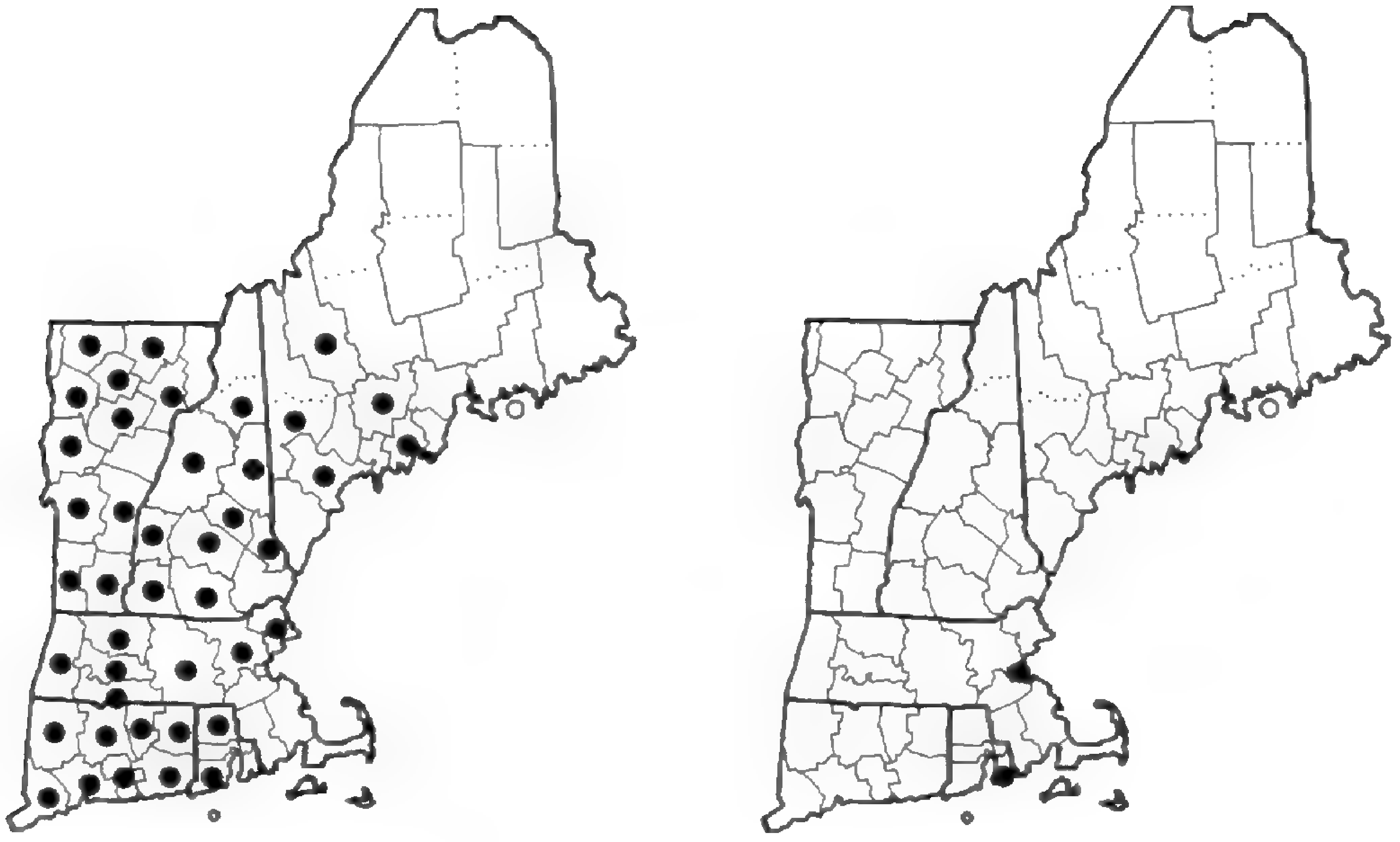
Elymus hystrix



ELYMUS PYCNANTHUS

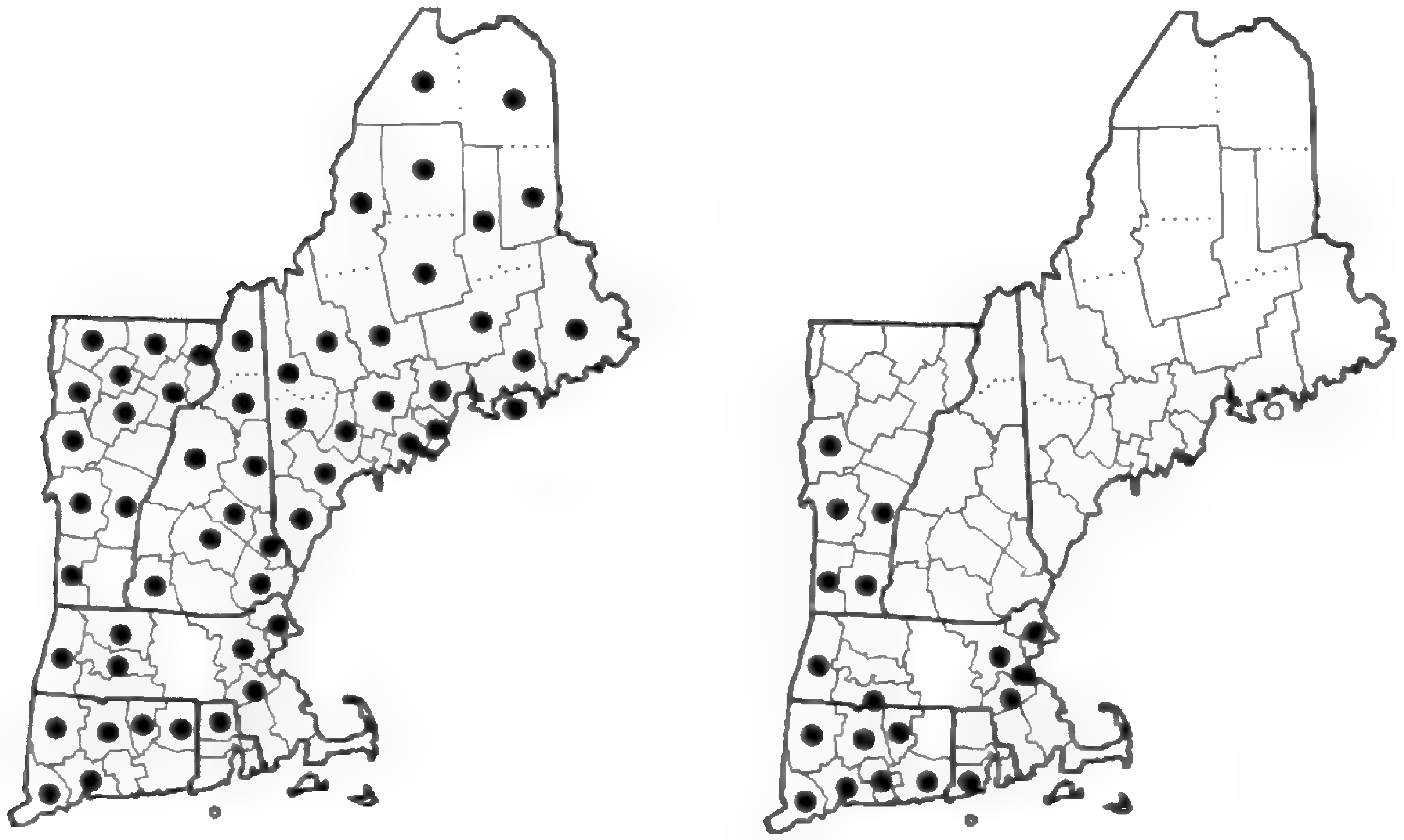
ELYMUS REPENS

Figure 32. Distribution maps for *Elymus glabriflorus*, *E. hystrix*, *E. PYCNANTHUS* and *E. REPENS*.



Elymus riparius

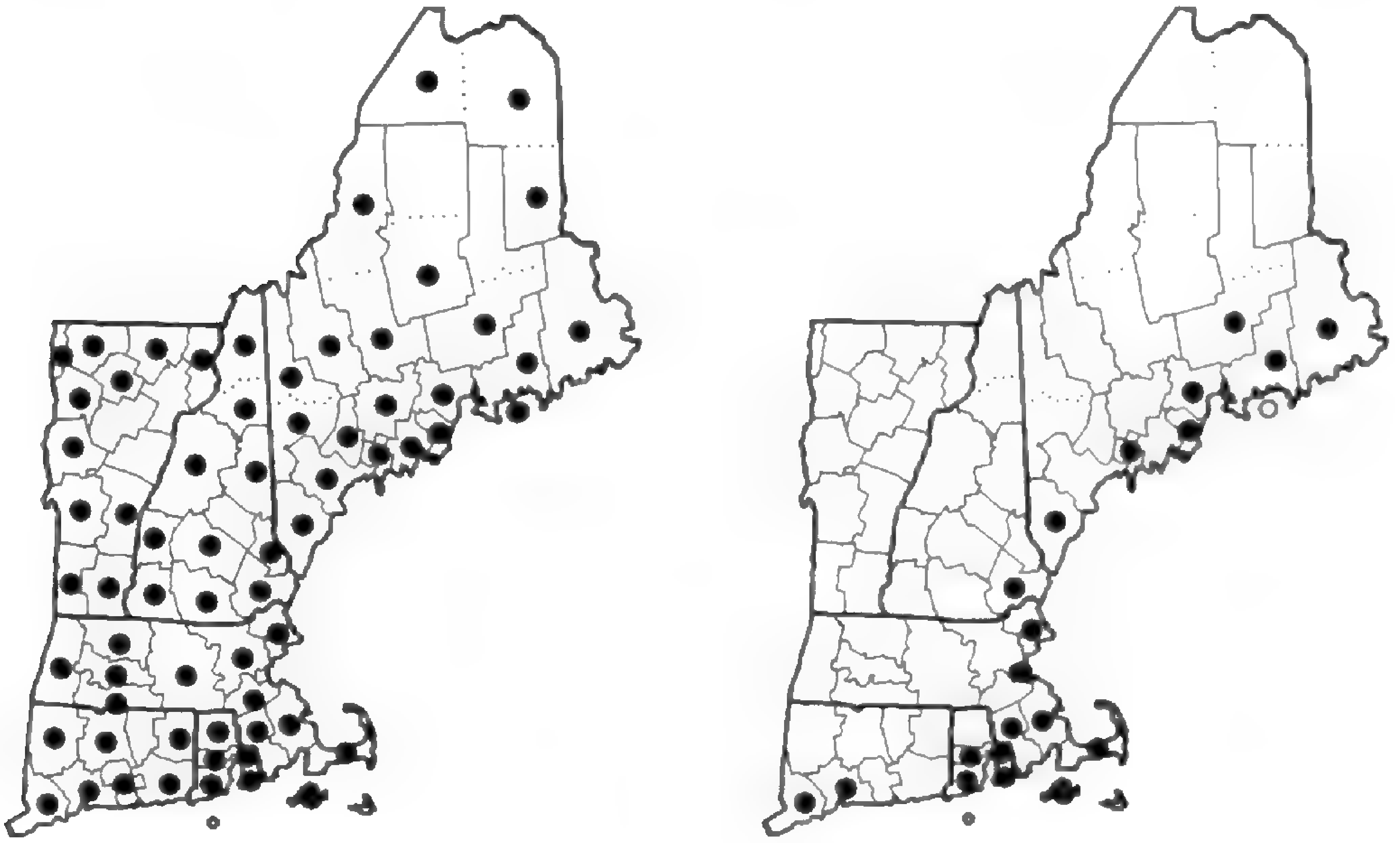
Elymus submuticus



Elymus trachycaulus
subsp. *trachycaulus*

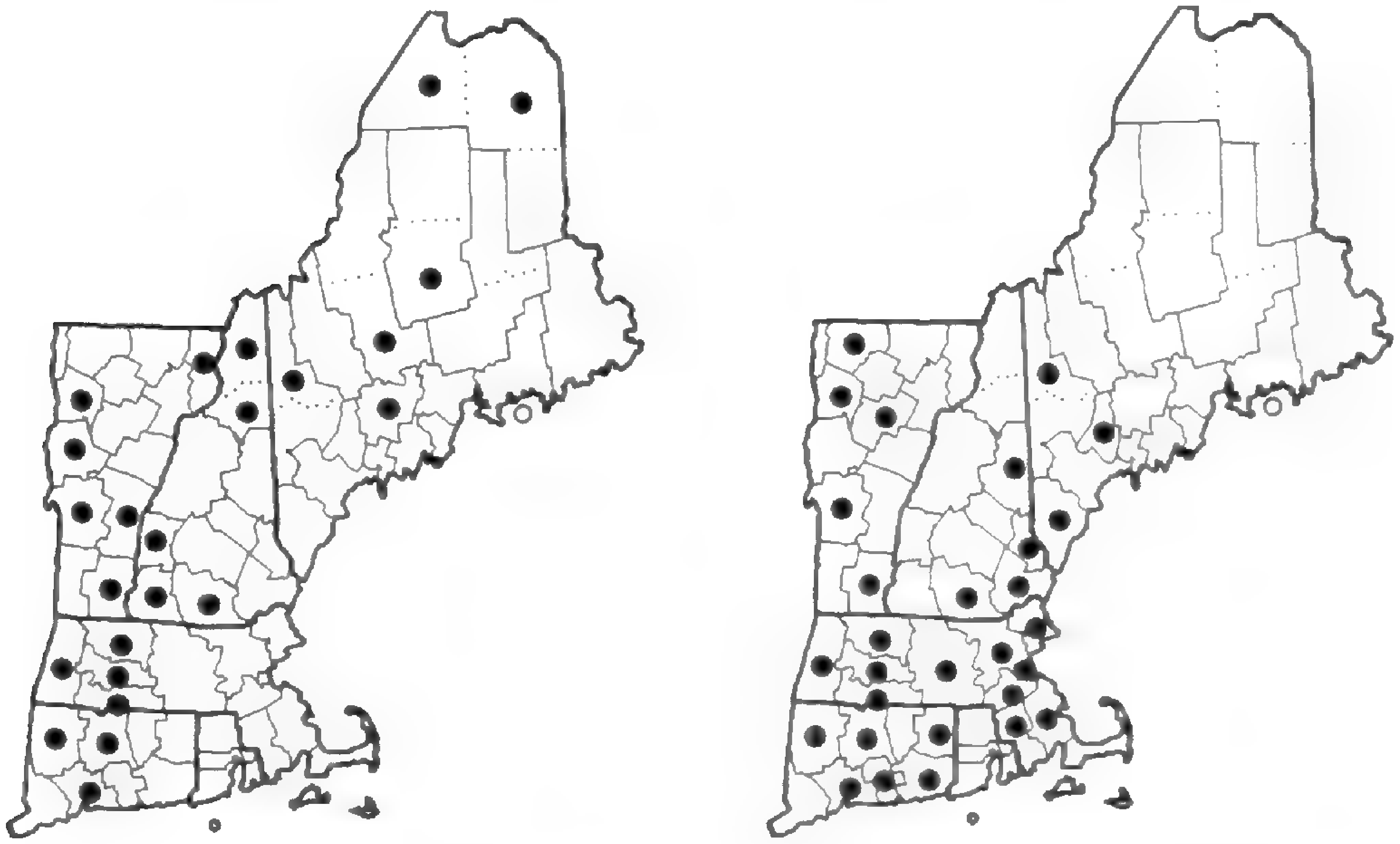
Elymus villosus

Figure 33. Distribution maps for *Elymus riparius, E. submuticus, E. trachycaulus* subsp. *trachycaulus* and *E. villosus.*



Elymus virginicus var. *virginicus*

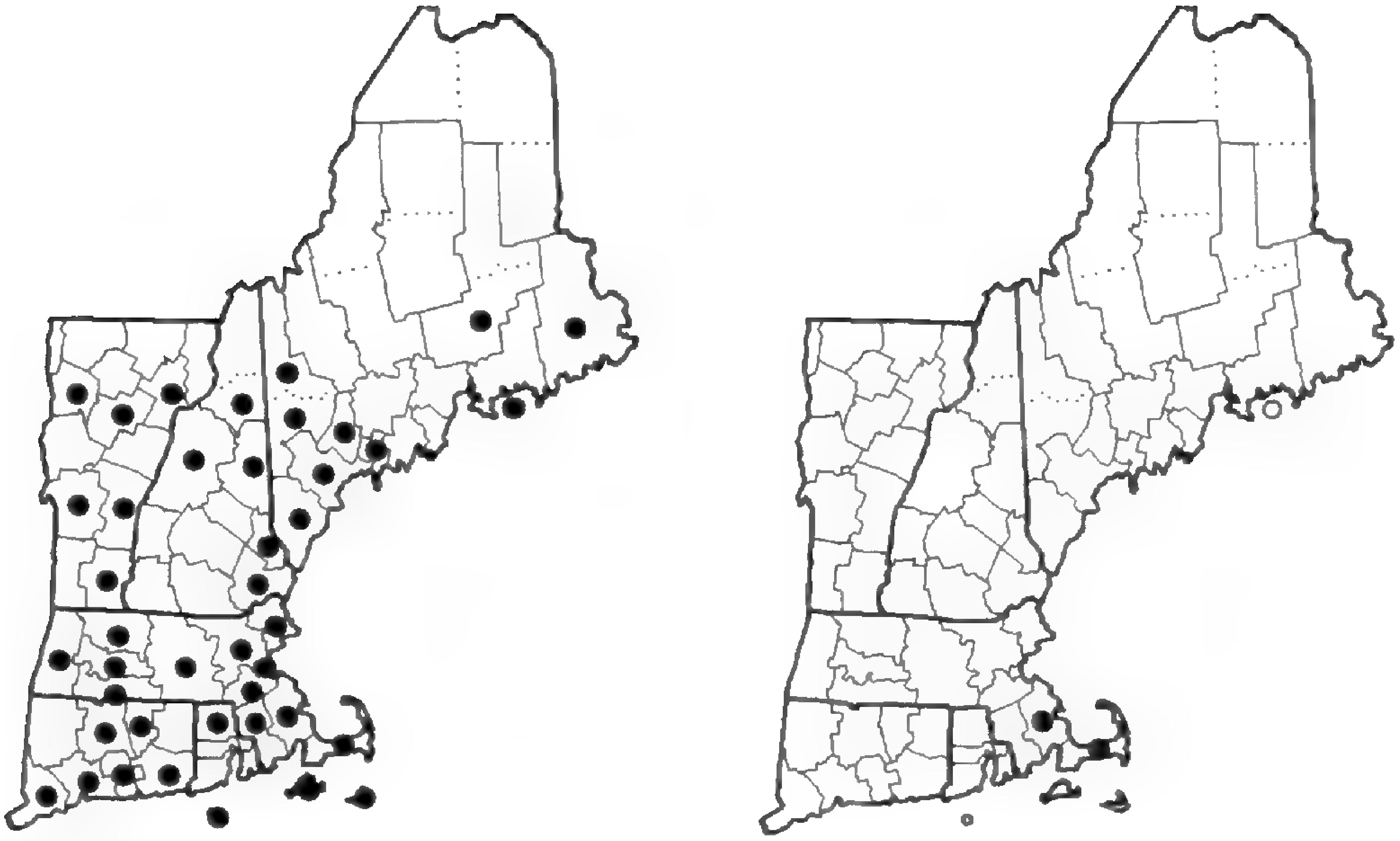
Elymus virginicus var. *halophilus*



Elymus wiegandii

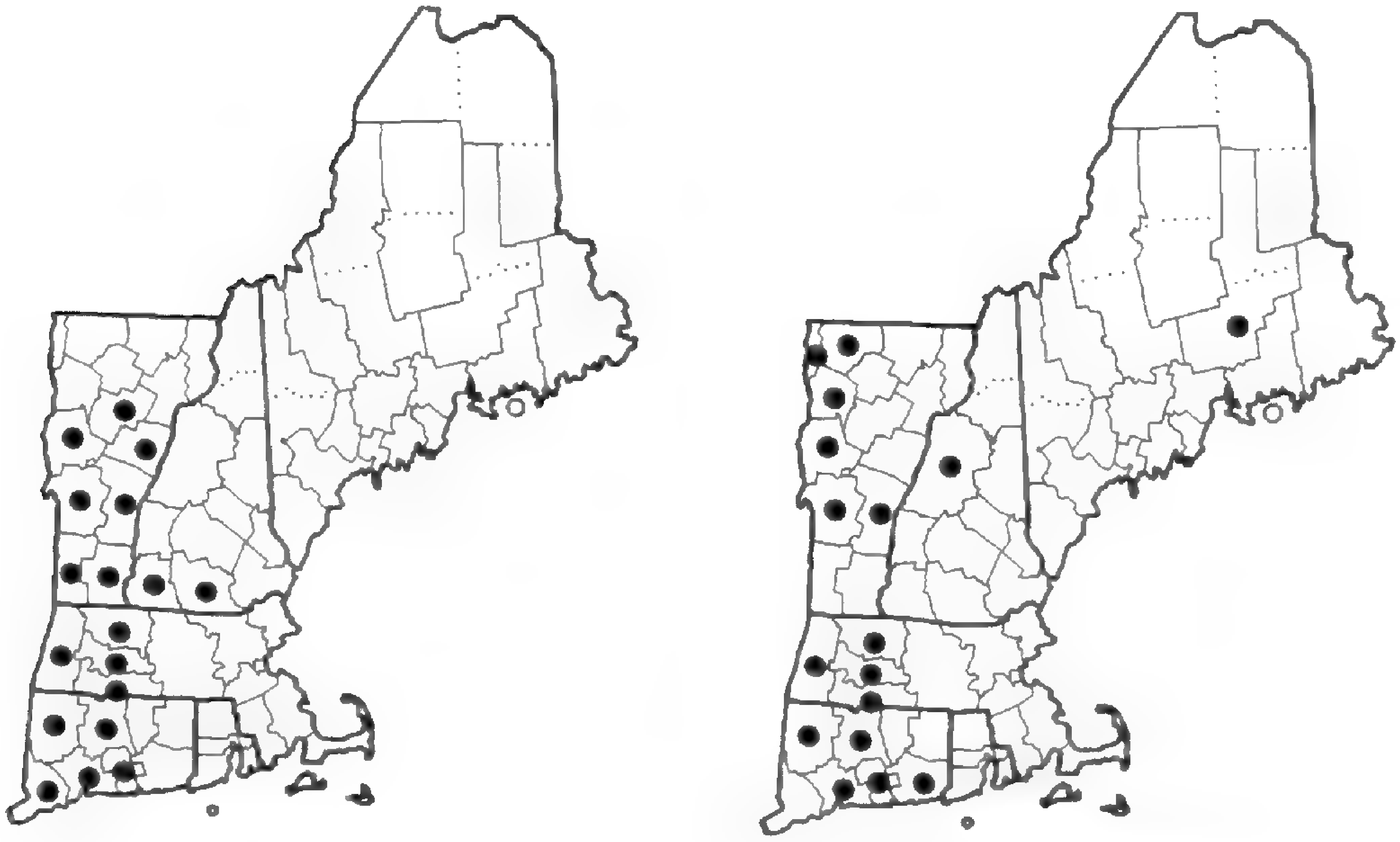
Eragrostis capillaris

Figure 34. Distribution maps for *Elymus virginicus* var. *virginicus*, *E. virginicus* var. *halophilus*, *E. wiegandii* and *Eragrostis capillaris*.



ERAGROSTIS CILIANENSIS

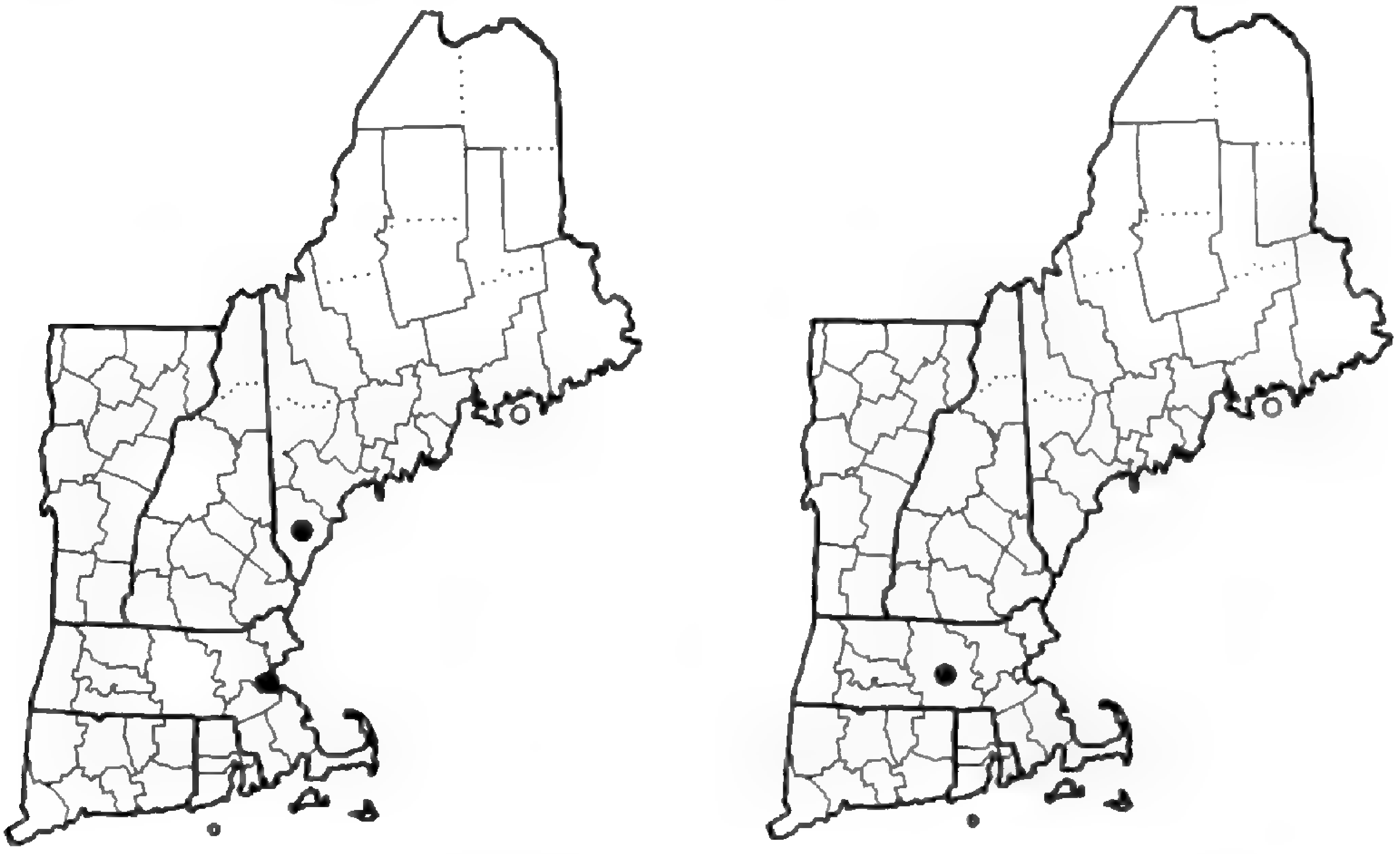
ERAGROSTIS CURVULA



Eragrostis frankii

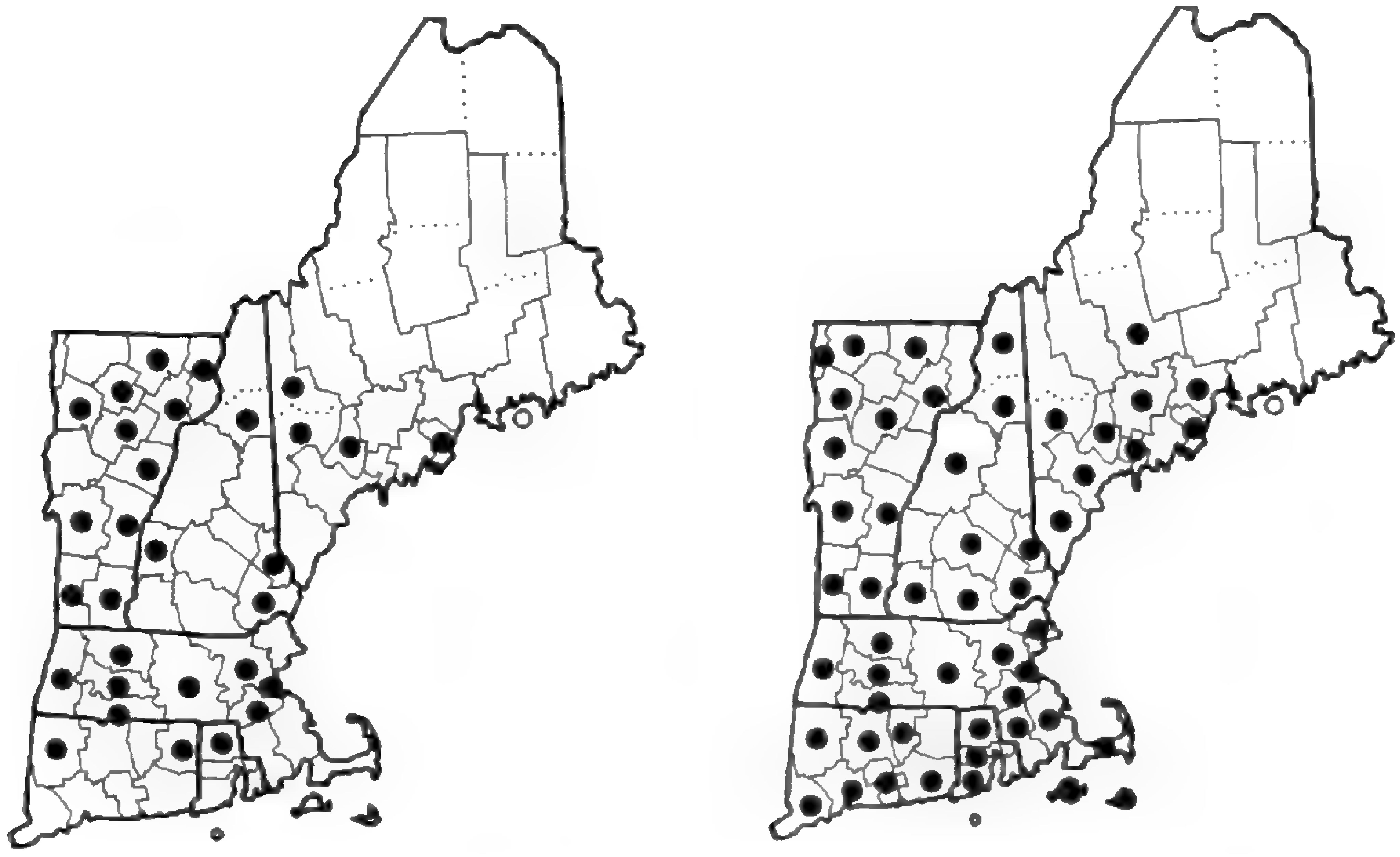
Eragrostis hypnoides

Figure 35. Distribution maps for *ERAGROSTIS CILIANENSIS, E. CURVULA, E. frankii* and *E. hypnoides.*



ERAGROSTIS INTERMEDIA

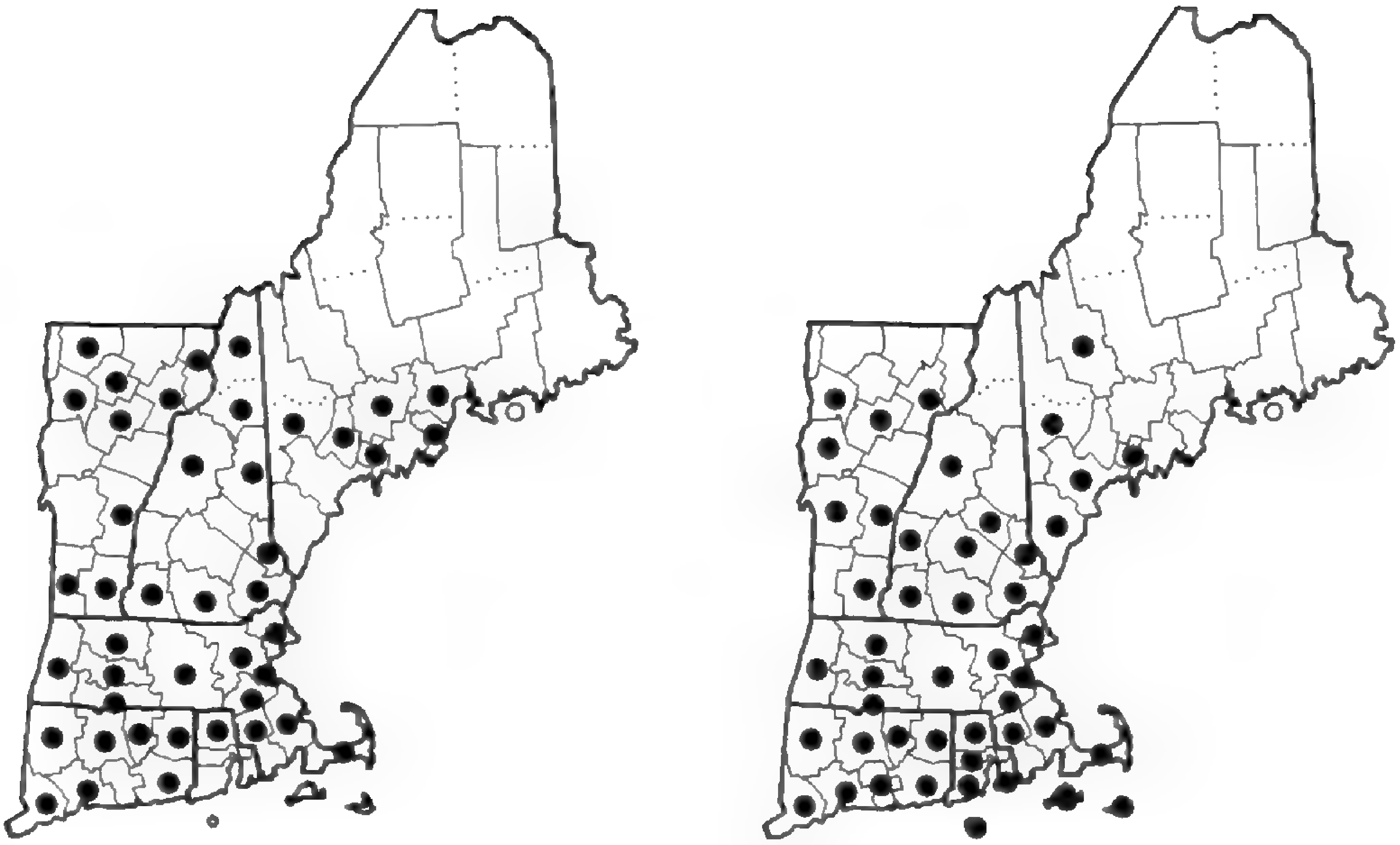
ERAGROSTIS MEXICANA subsp. *VIRESCENS*



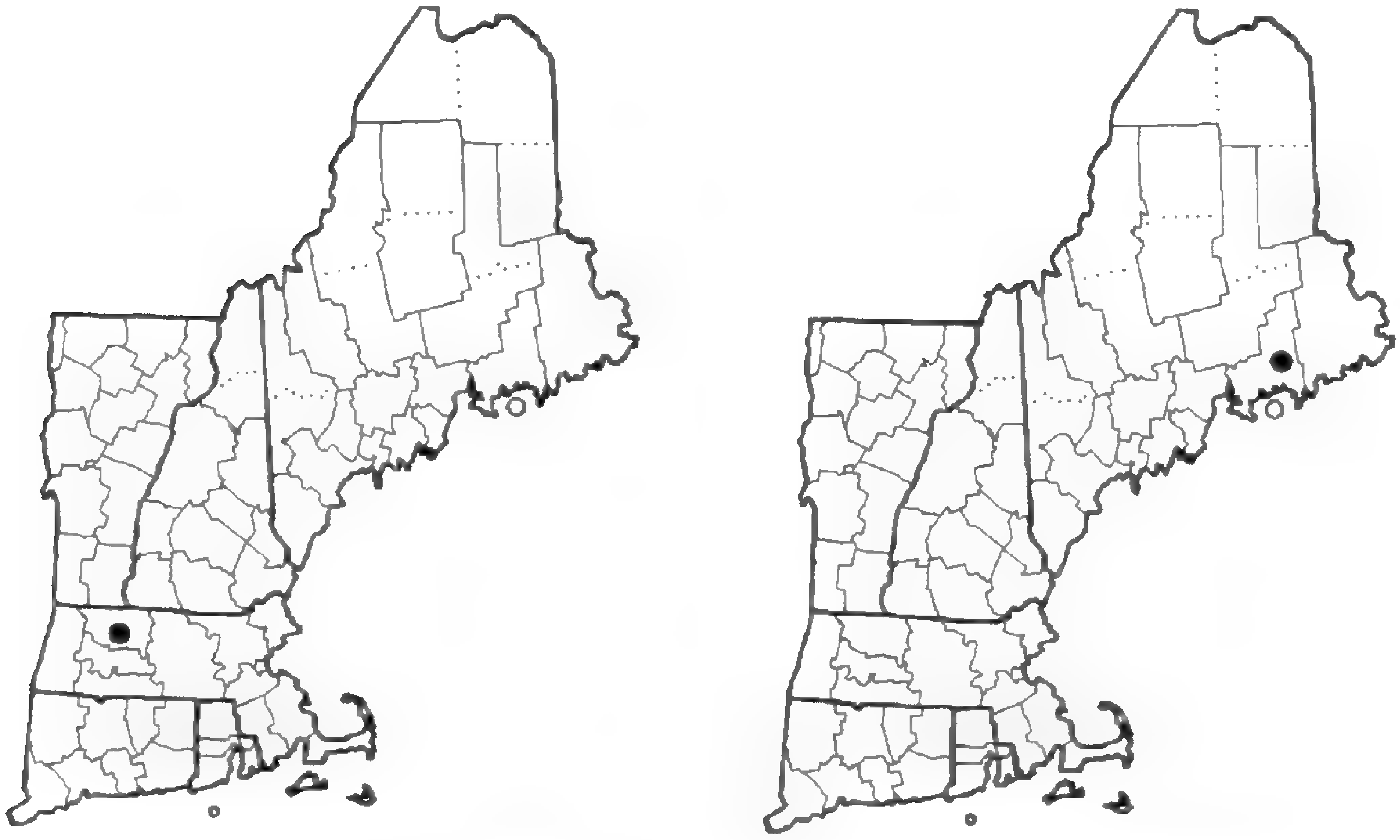
ERAGROSTIS MINOR

Eragrostis pectinacea

Figure 36. Distribution maps for *ERAGROSTIS INTERMEDIA*, *E. MEXICANA* subsp. *VIRESCENS*, *E. MINOR* and *E. pectinacea*.

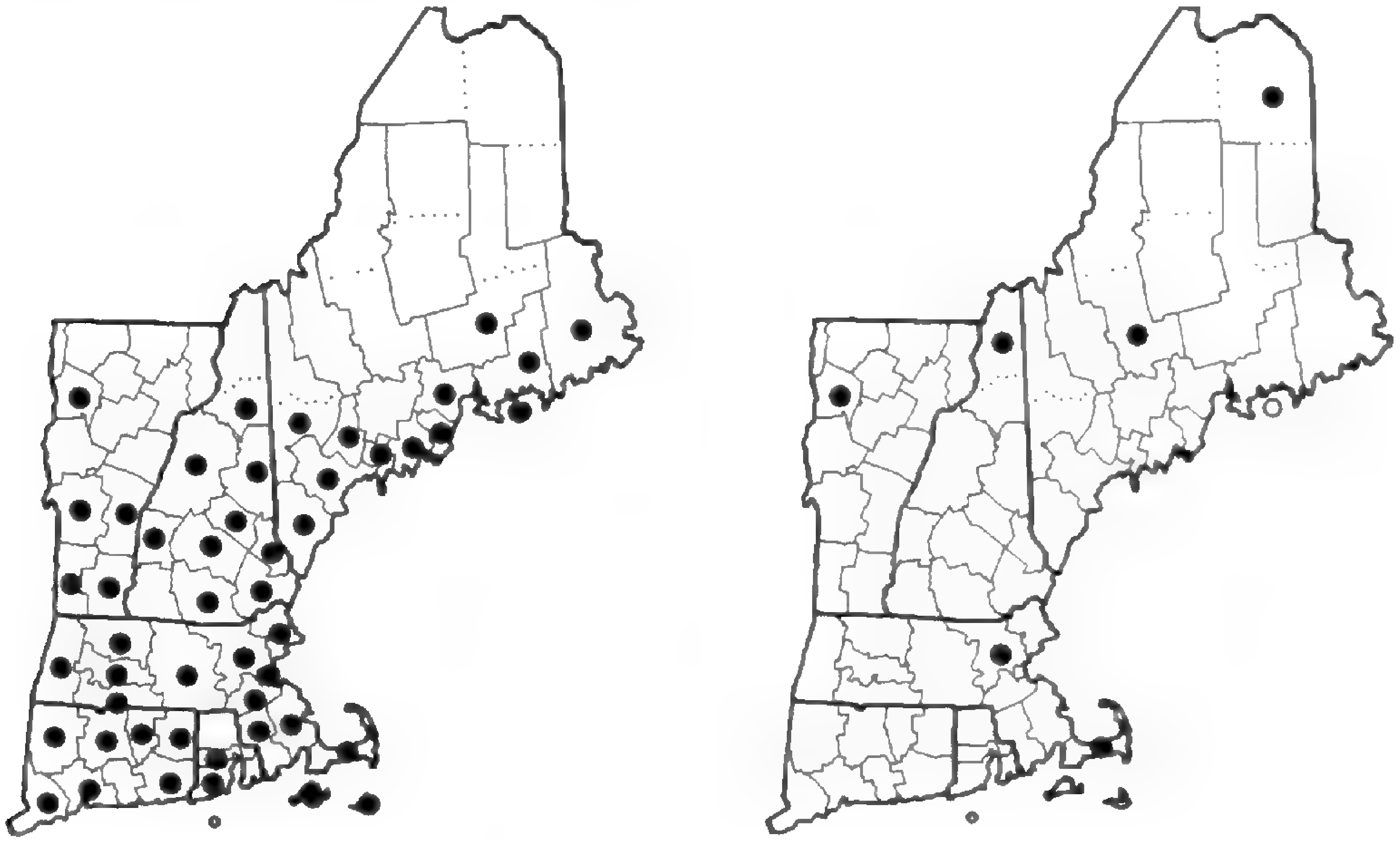


ERAGROSTIS PILOSA *Eragrostis spectabilis*

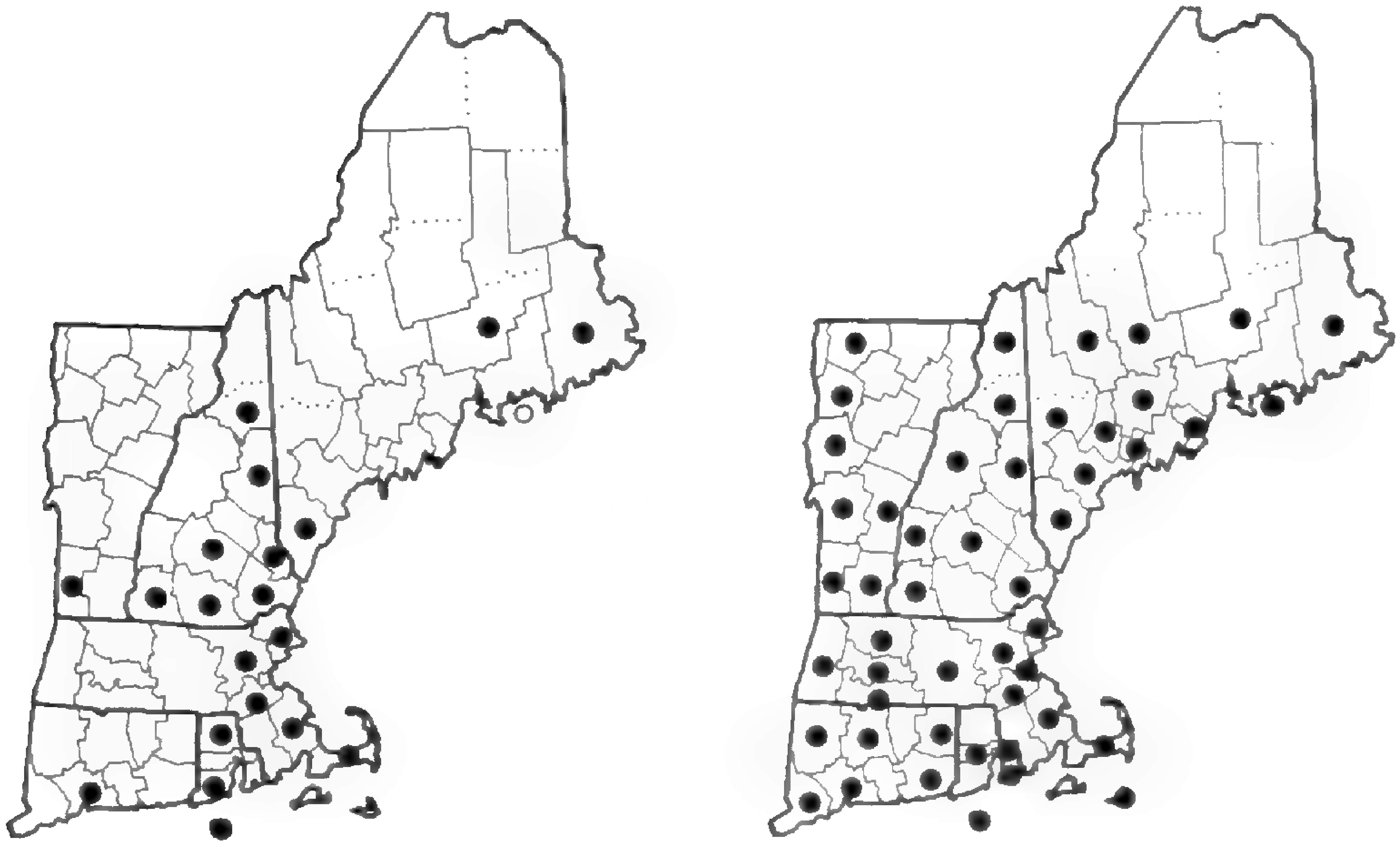


EREMOCHLOA OPHIUROIDES *Festuca brachyphylla*

Figure 37. Distribution maps for *ERAGROSTIS PILOSA, E. spectabilis, EREMOCHLOA OPHIUROIDES* and *Festuca brachyphylla.*

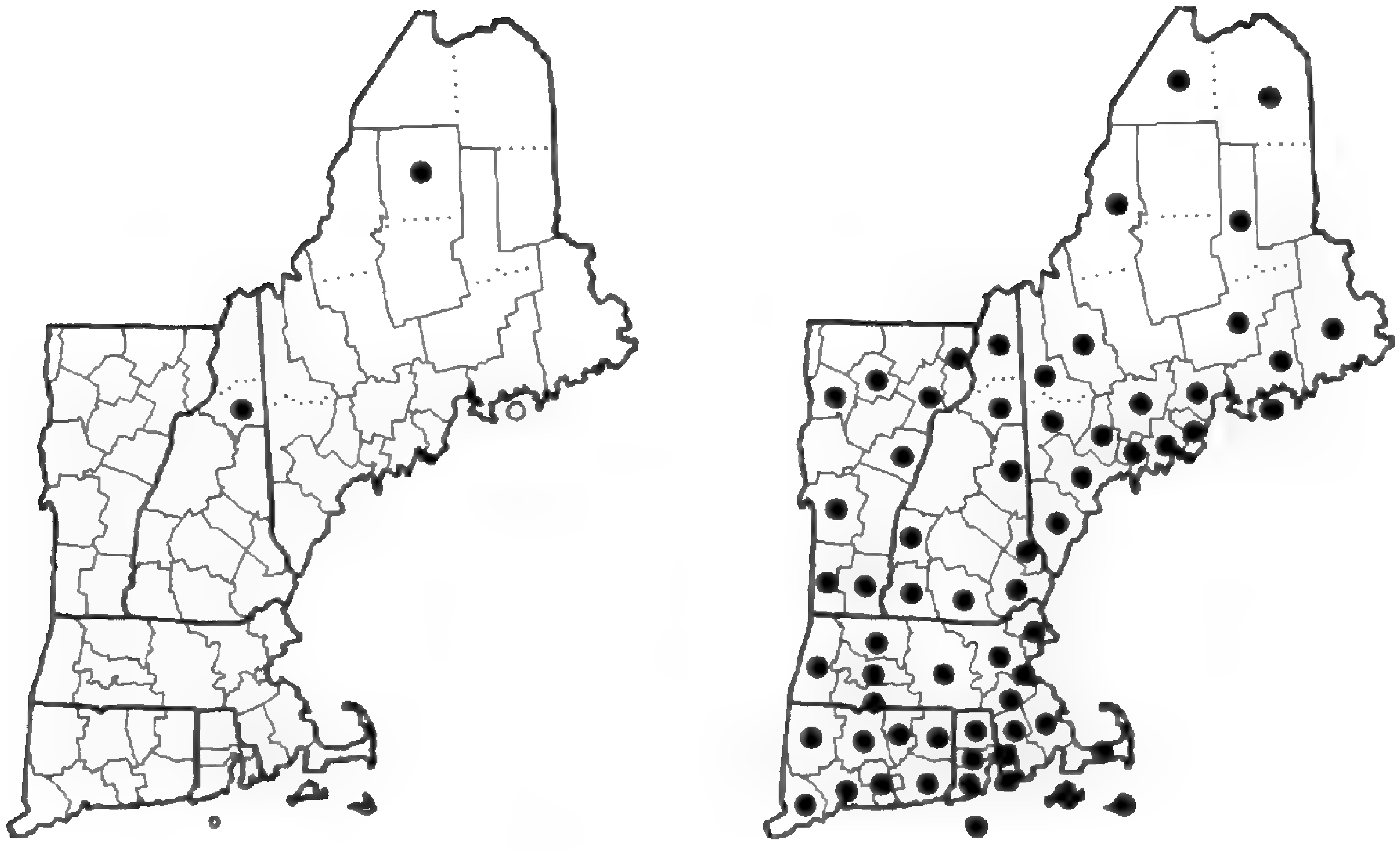


FESTUCA FILIFORMIS *FESTUCA HETEROMALLA*



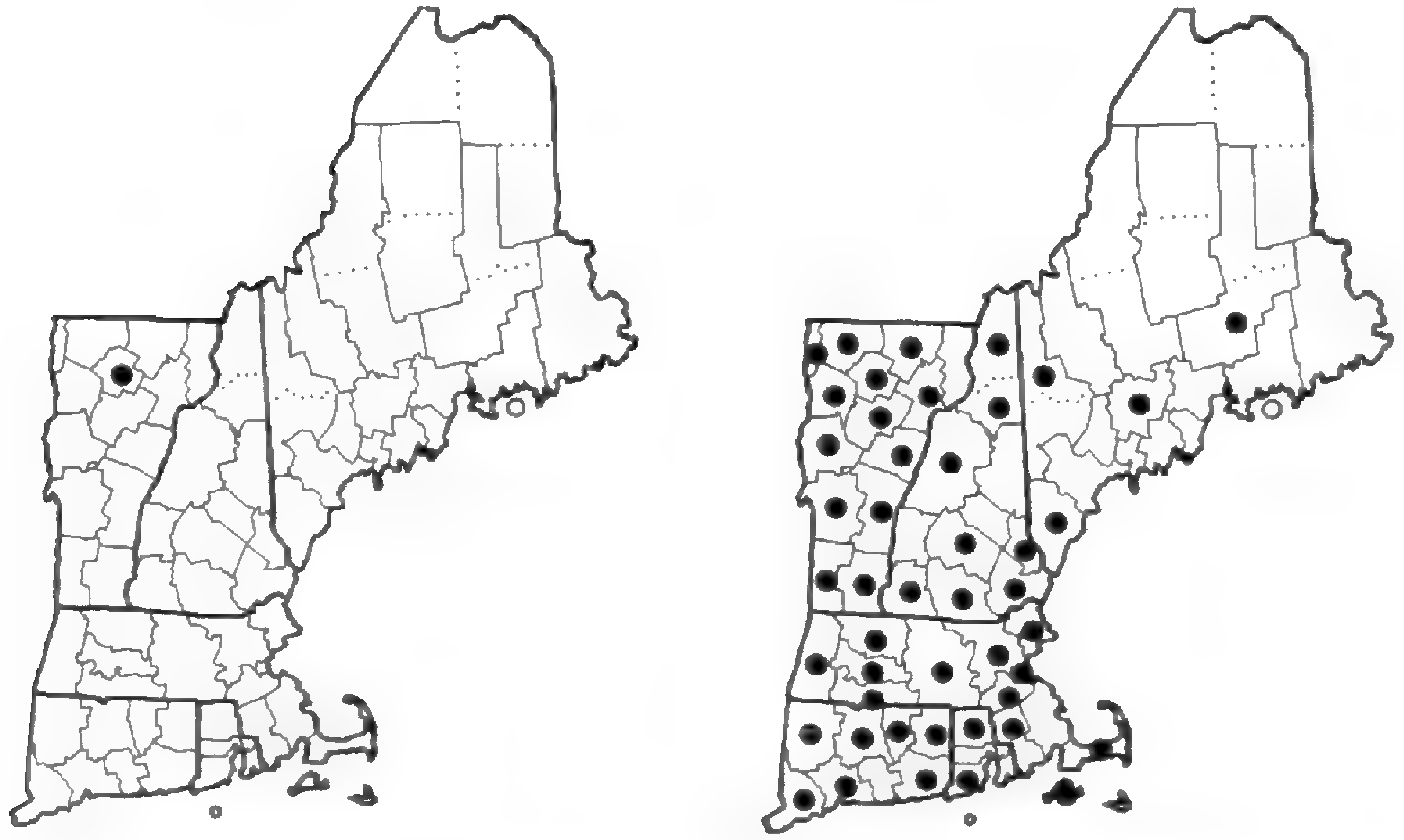
FESTUCA NIGRESCENS *FESTUCA OVINA*

Figure 38. Distribution maps for *FESTUCA FILIFORMIS*, *F. HETEROMALLA*, *F. NIGRESCENS* and *F. OVINA*.



Festuca prolifera

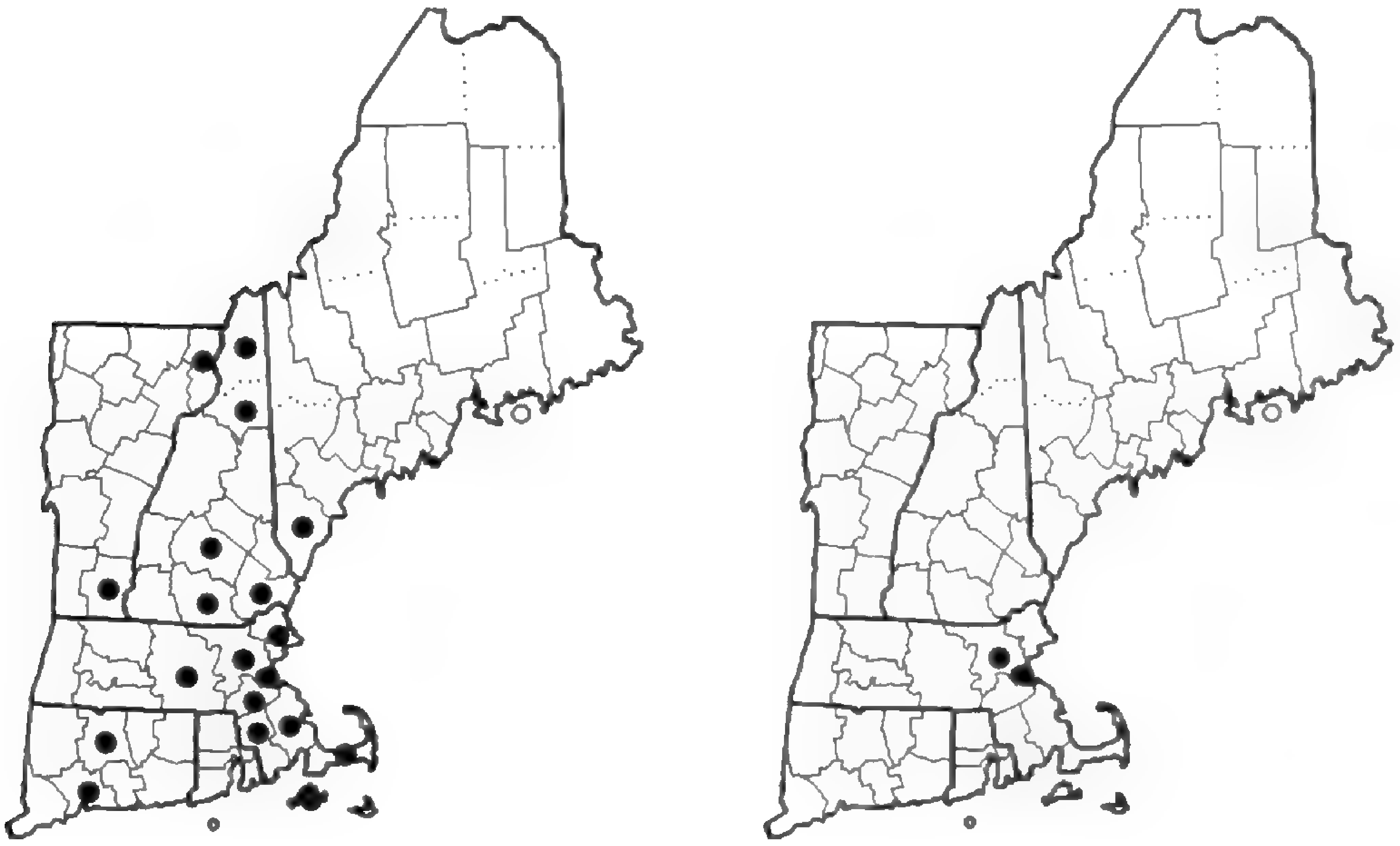
FESTUCA RUBRA
subsp. *RUBRA*



Festuca saximontana

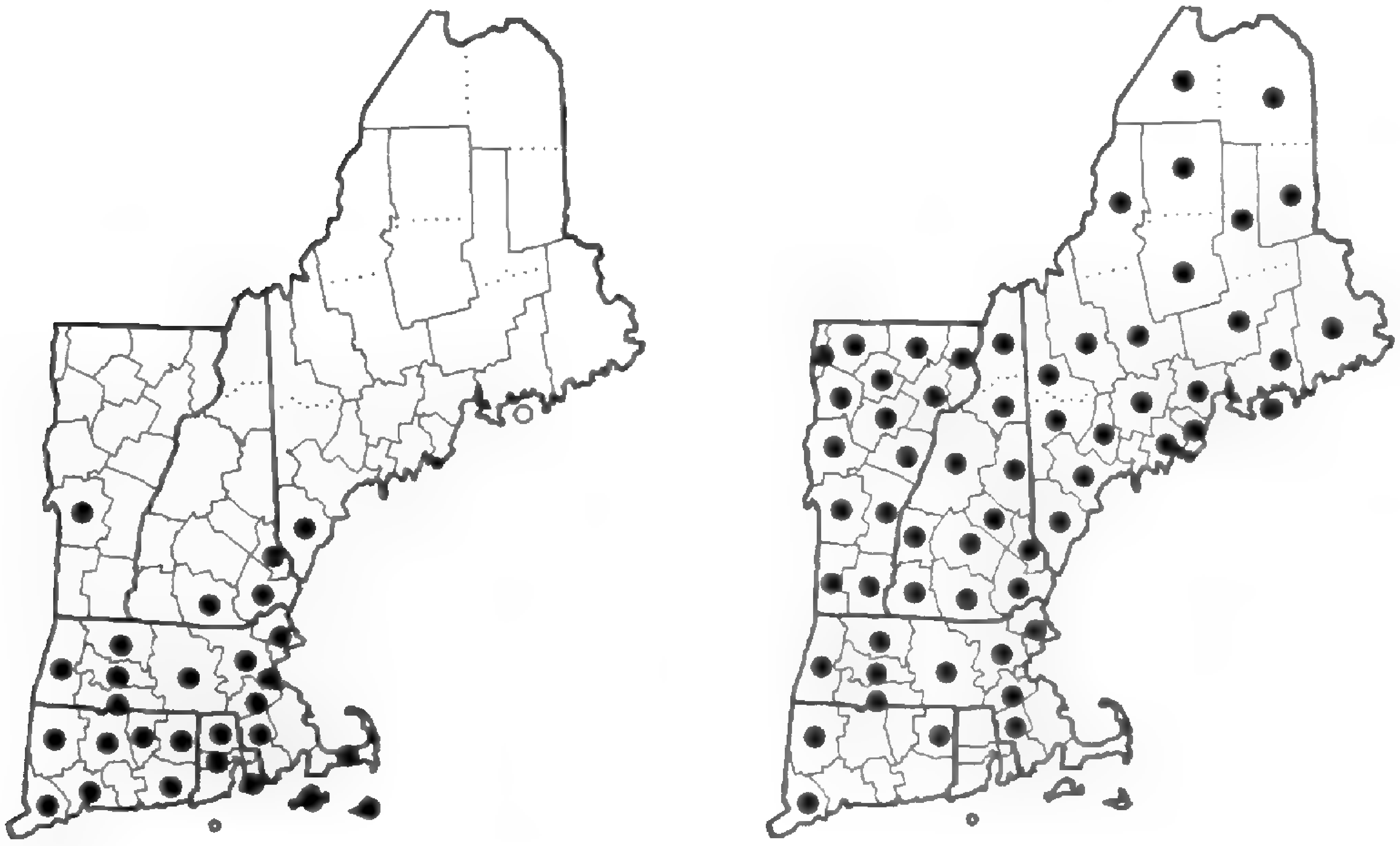
Festuca subverticillata

Figure 39. Distribution maps for *Festuca prolifera, F. RUBRA* subsp. *RUBRA, F. saximontana* and *F. subverticillata.*



FESTUCA TRACHYPHYLLA

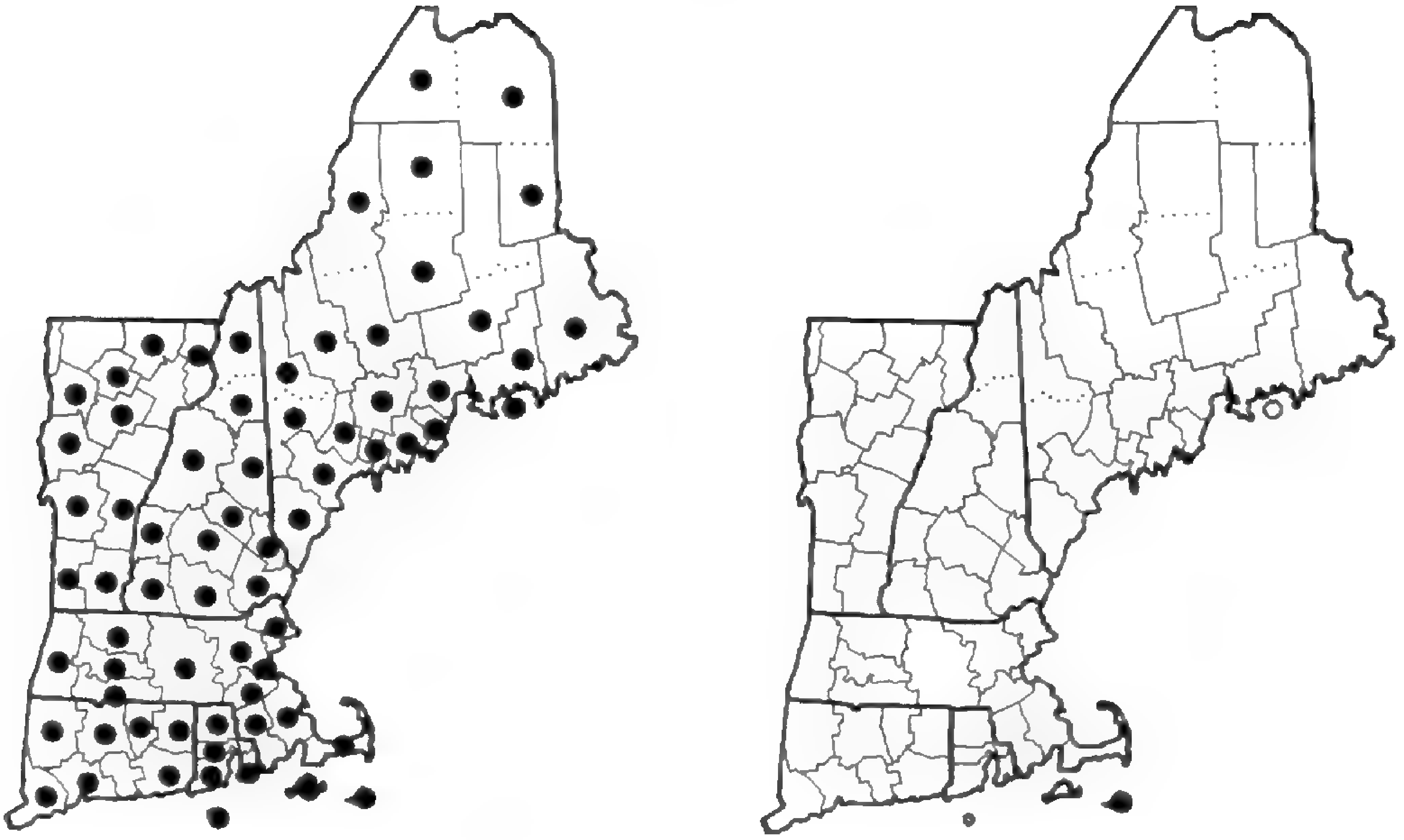
GASTRIDIUM PHLEOIDES



Glyceria acutiflora

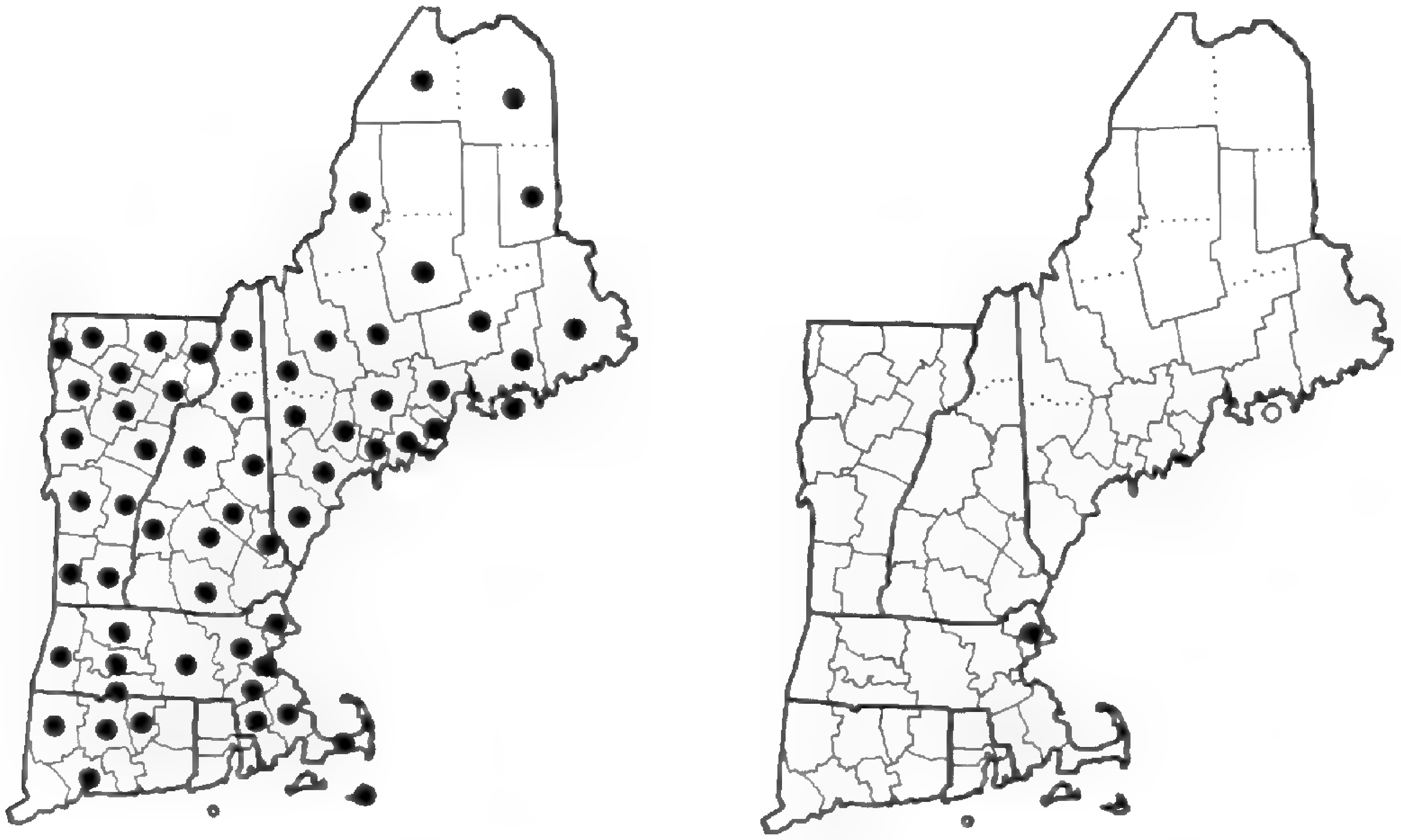
Glyceria borealis

Figure 40. Distribution maps for *FESTUCA TRACHYPHYLLA*, *GASTRIDIUM PHLEOIDES*, *Glyceria acutiflora* and *G. borealis*.



Glyceria canadensis

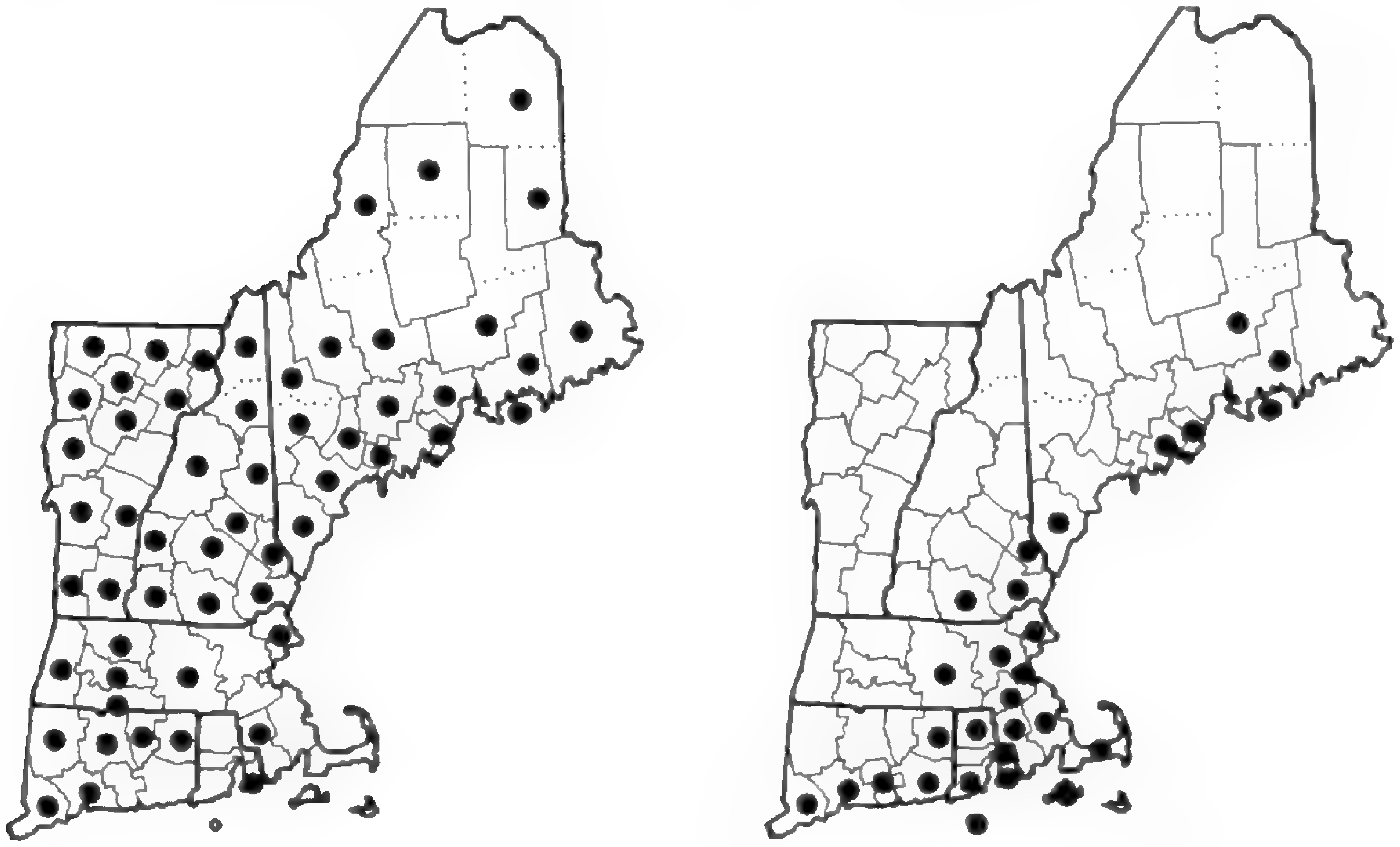
Glyceria fluitans



Glyceria grandis

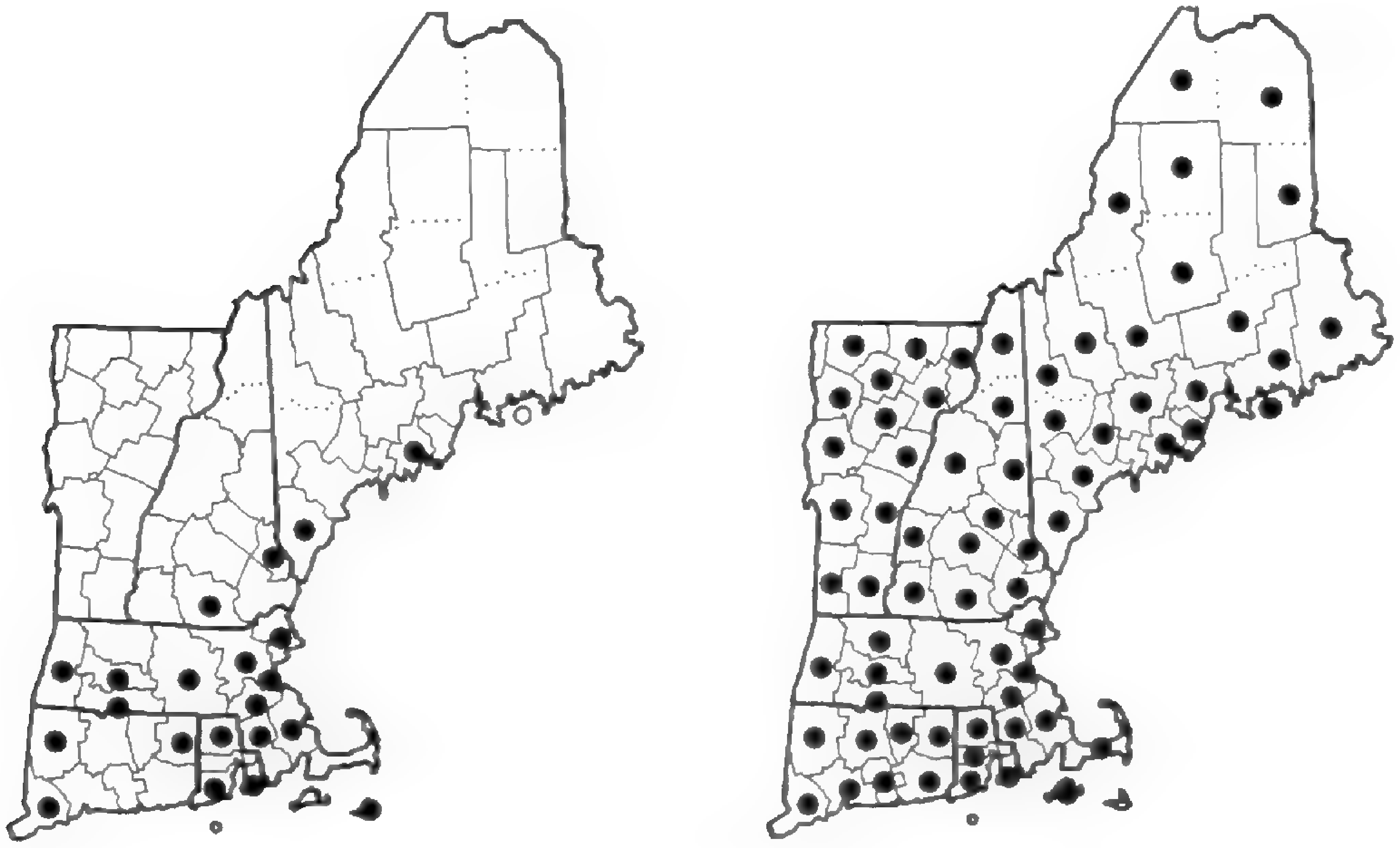
GLYCERIA MAXIMA

Figure 41. Distribution maps for *Glyceria canadensis, G. fluitans, G. grandis* and *G. MAXIMA*.



Glyceria melicaria

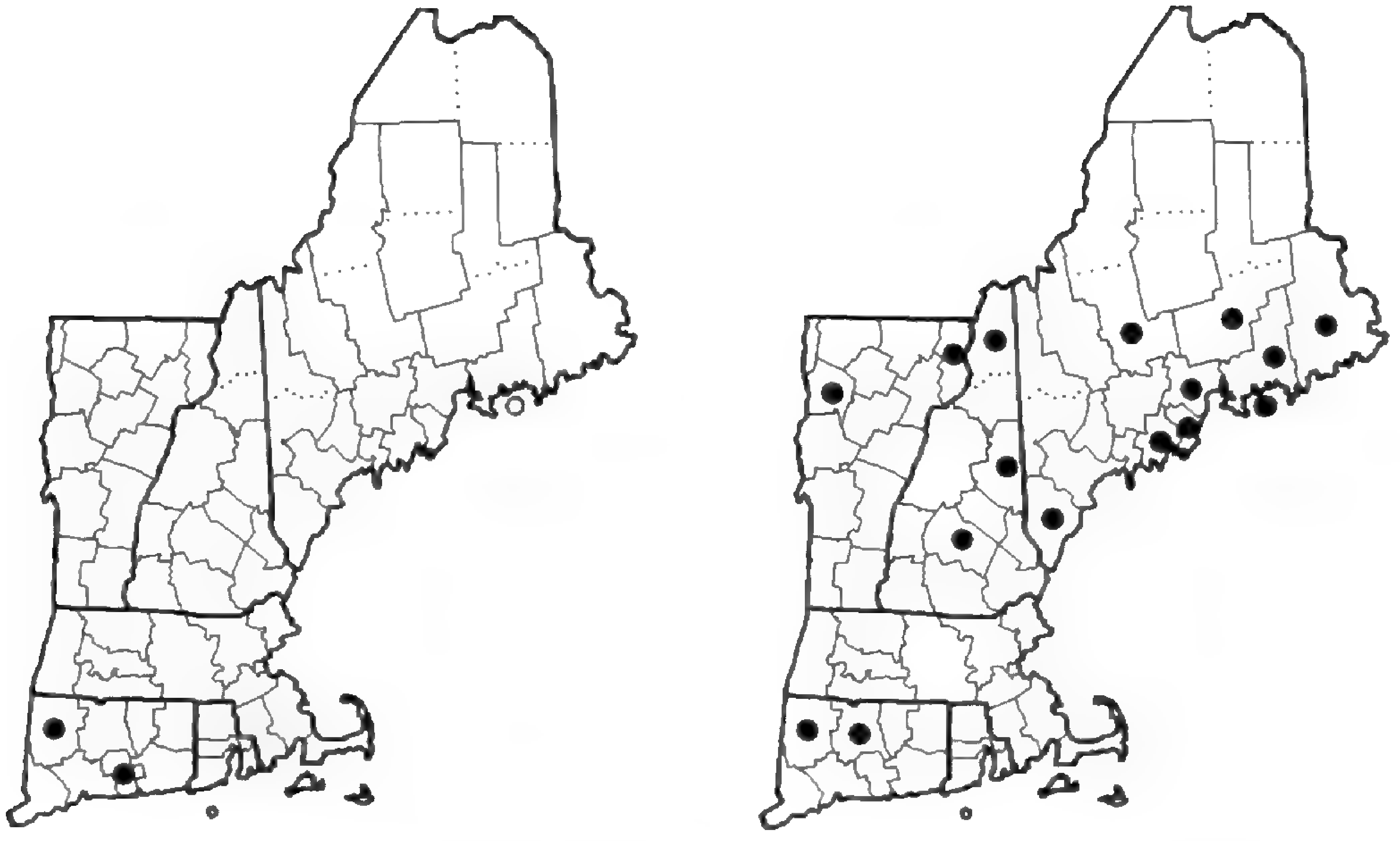
Glyceria obtusa



Glyceria septentrionalis

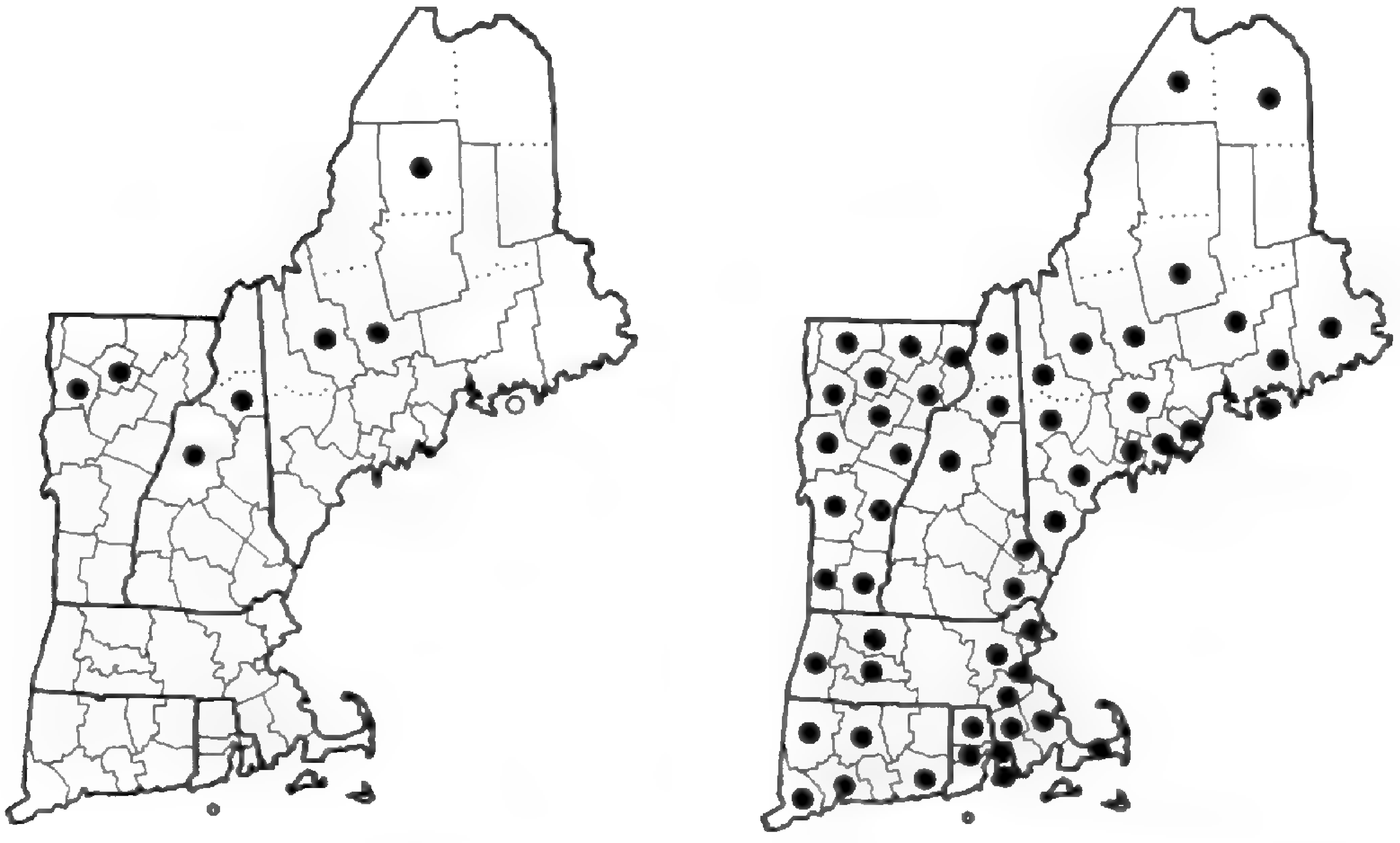
Glyceria striata

Figure 42. Distribution maps for *Glyceria melicaria, G. obtusa, G. septentrionalis* and *G. striata.*



Glyceria acutiflora x *G. septentrionalis*

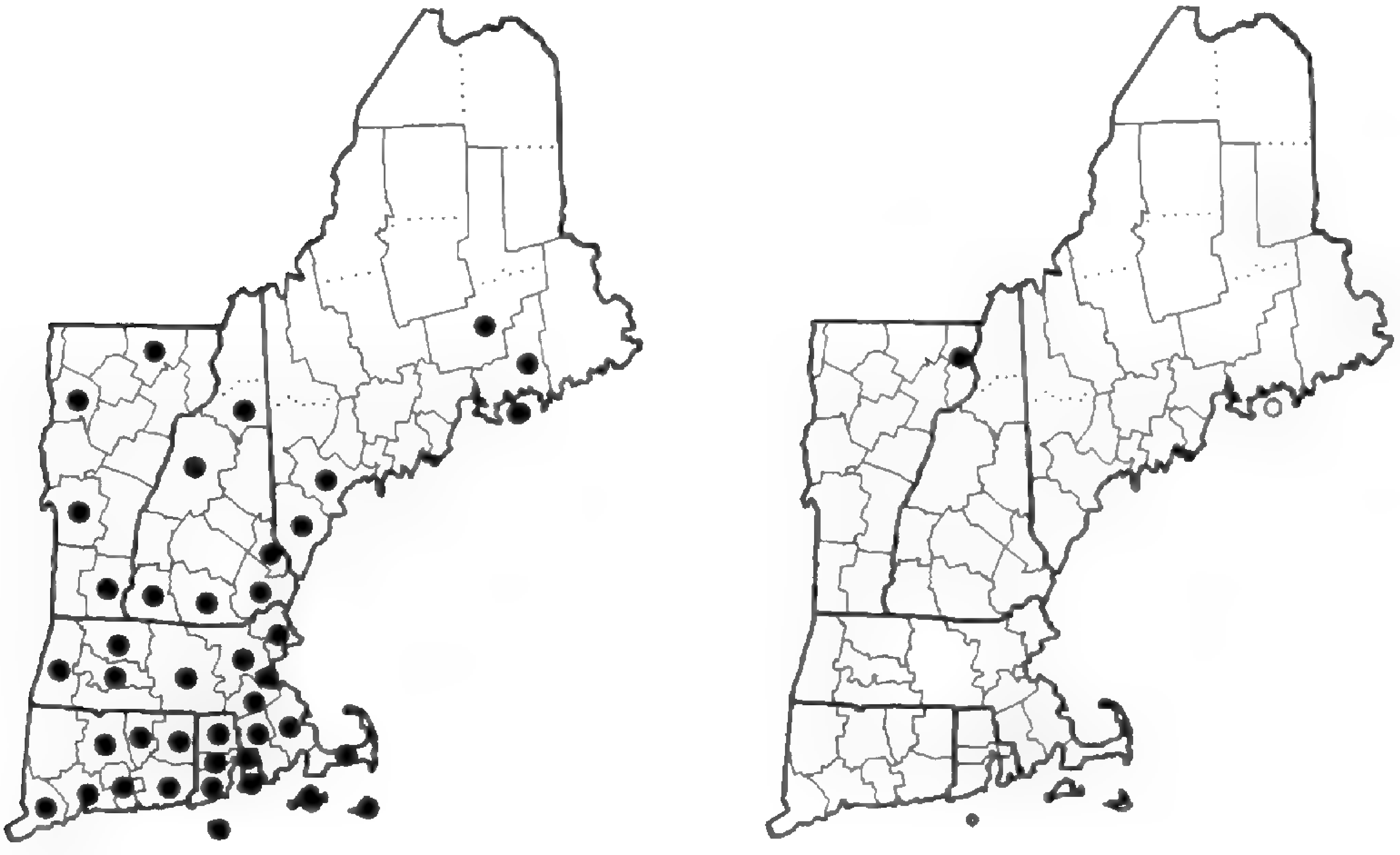
Glyceria x *laxa*



Hierochloë alpina
subsp. *orthantha*

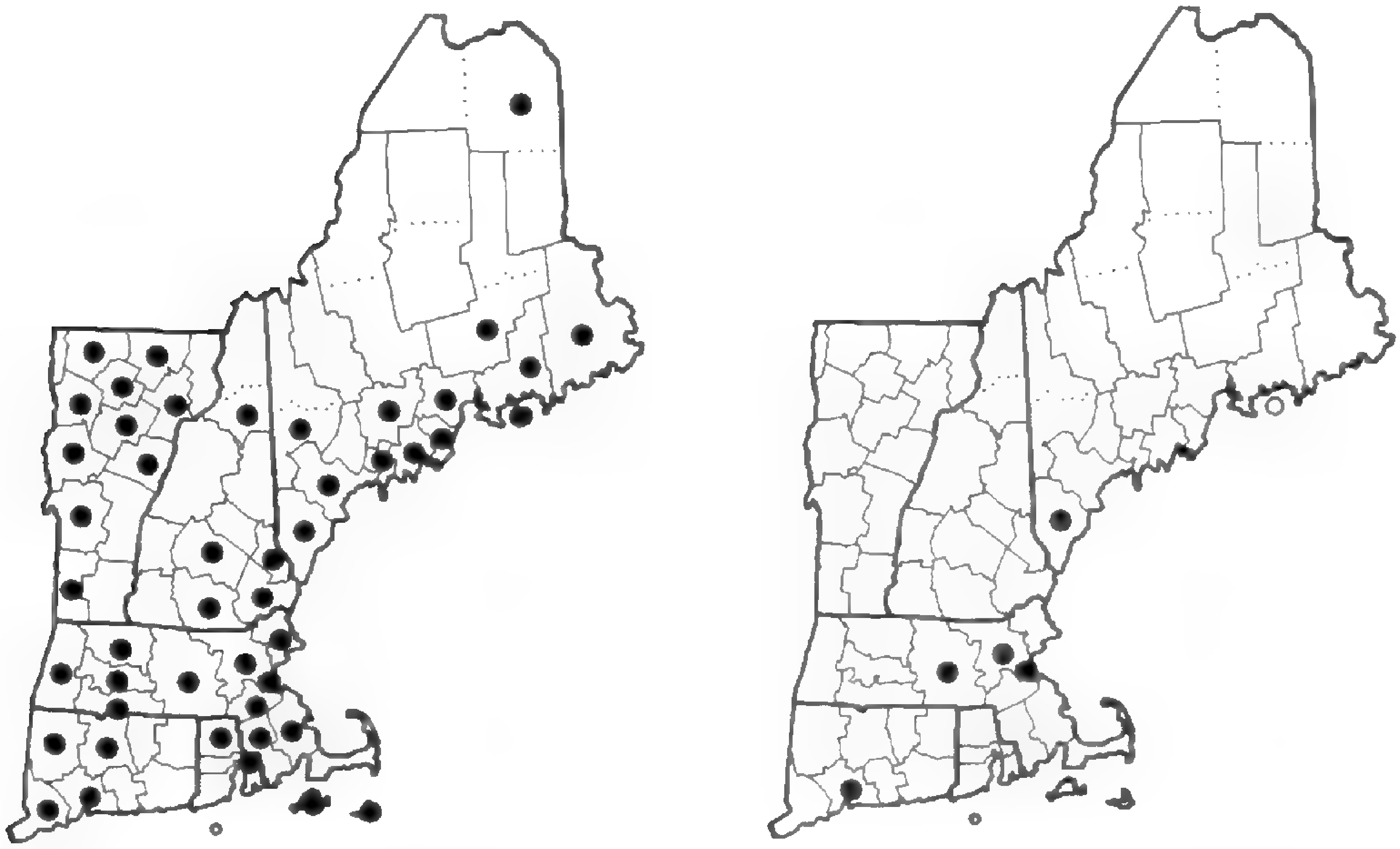
Hierochloë odorata

Figure 43. Distribution maps for *Glyceria acutiflora* × *G. septentrionalis*, *G.* × *laxa*, *Hierochloë alpina* subsp. *orthantha* and *H. odorata*.



HOLCUS LANATUS

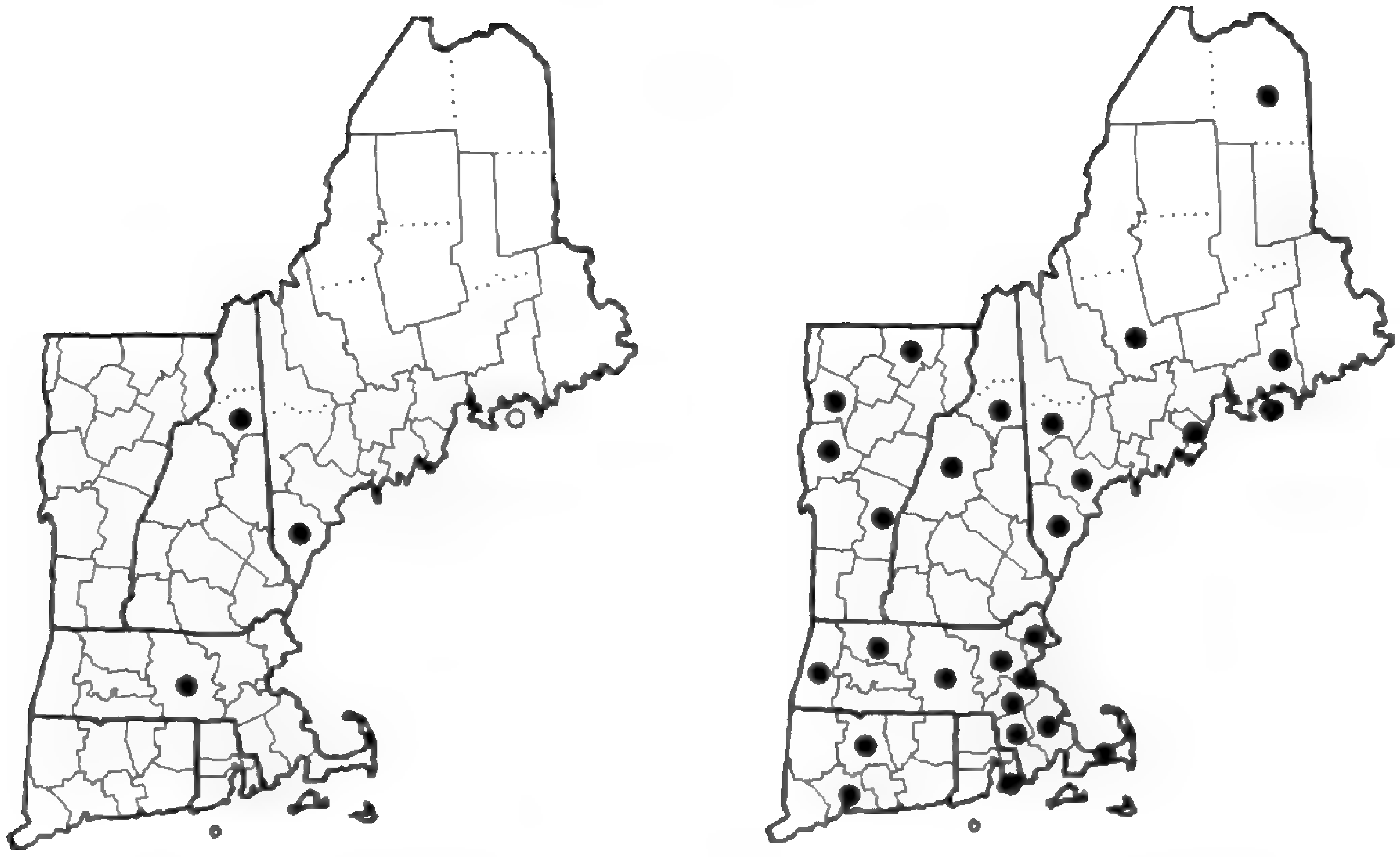
HOLCUS MOLLIS



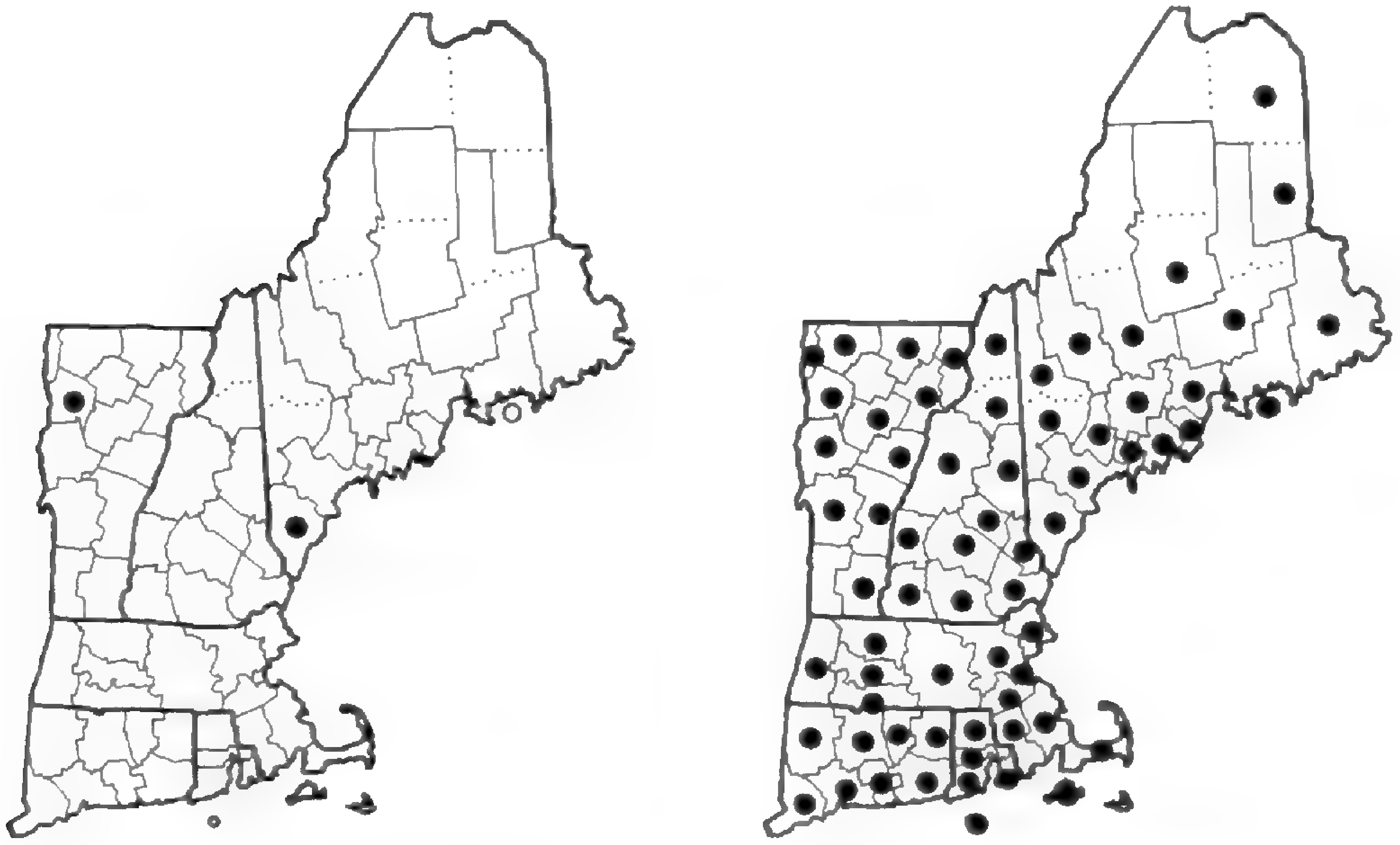
Hordeum jubatum

HORDEUM MURINUM
subsp. *LEPORINUM*

Figure 44. Distribution maps for *HOLCUS LANATUS*, *H. MOLLIS*, *Hordeum jubatum* and *H. MURINUM* subsp. *LEPORINUM*.

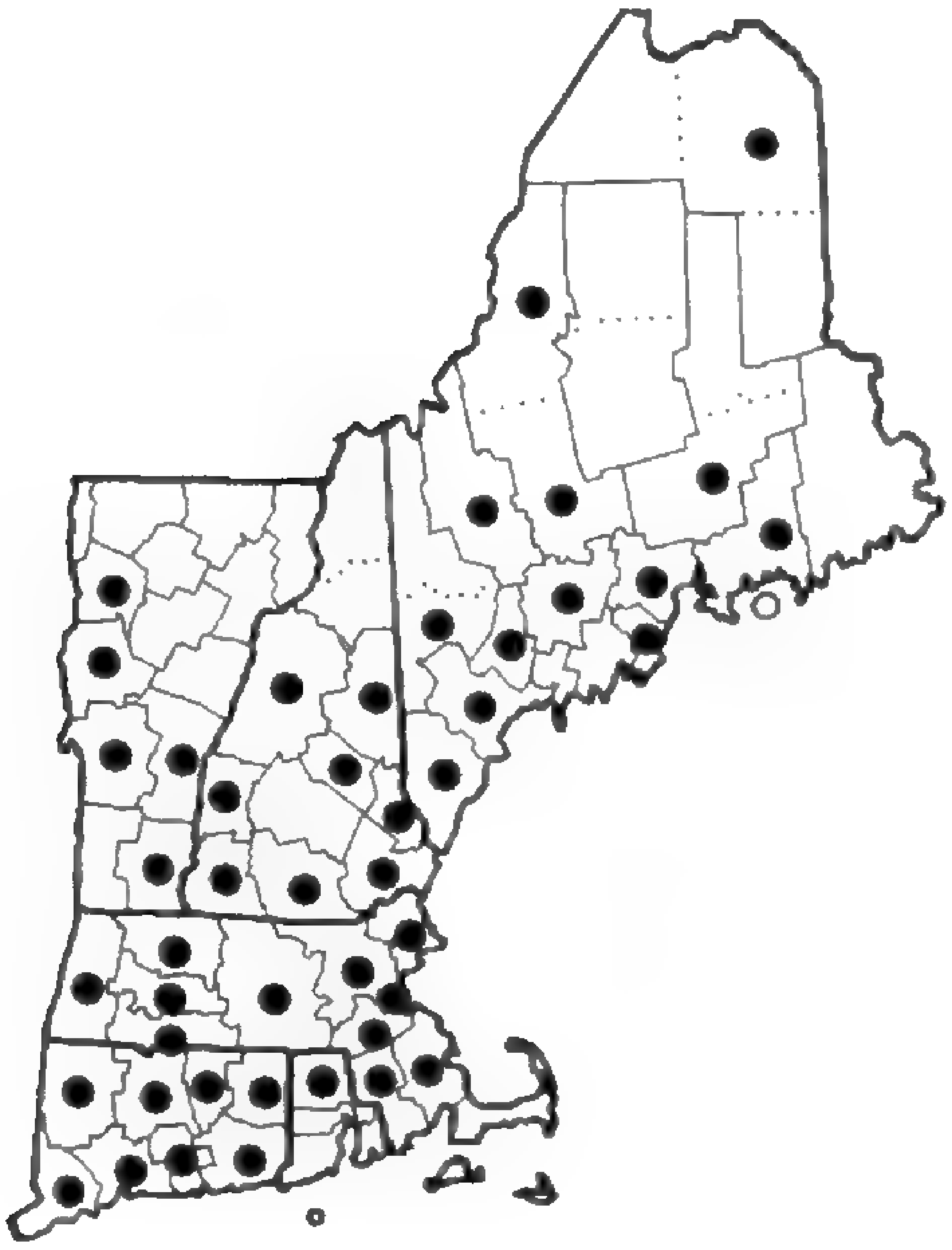


HORDEUM PUSILLUM *HORDEUM VULGARE*

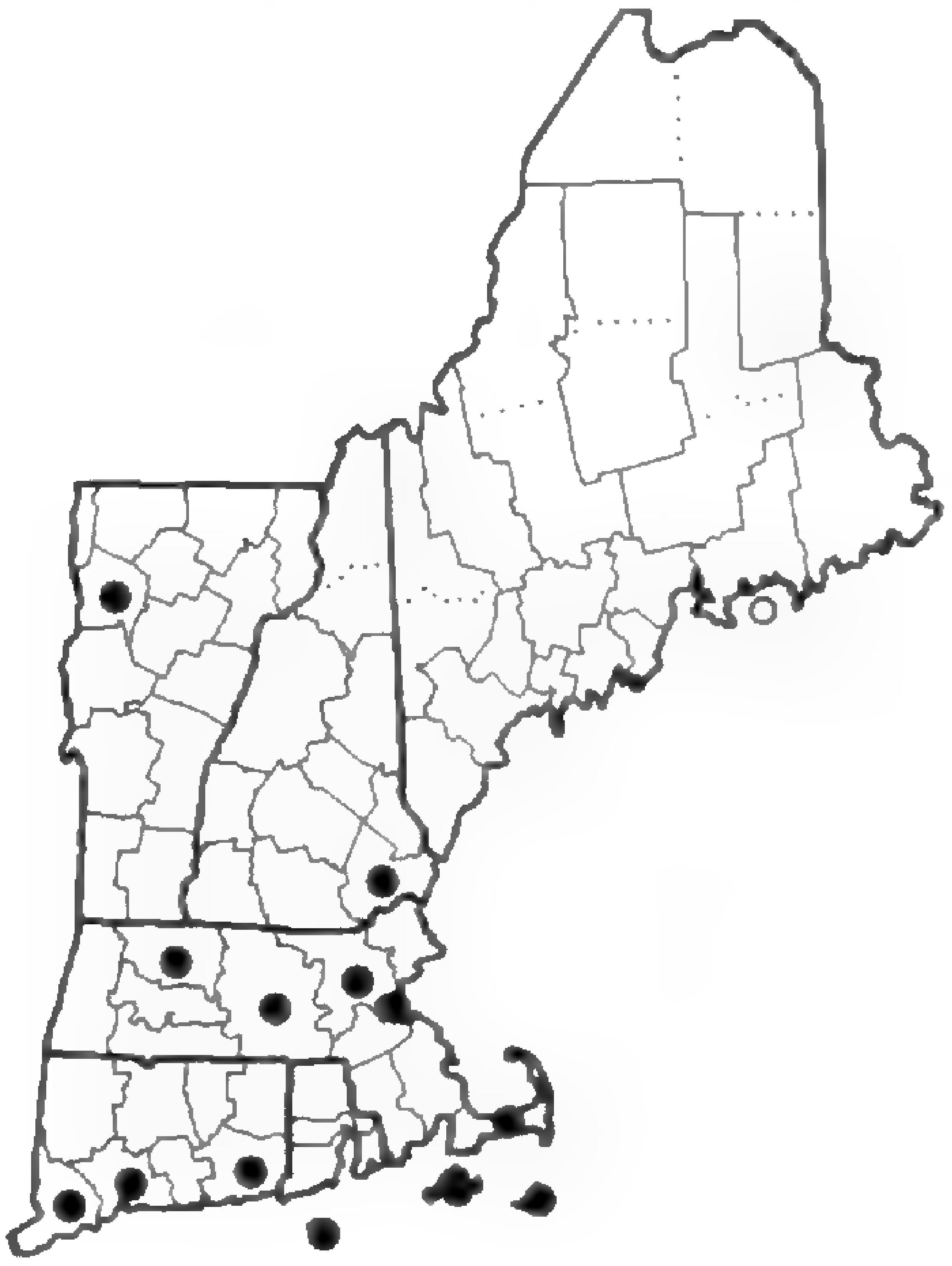


KOELERIA MACRANTHA *Leersia oryzoides*

Figure 45. Distribution maps for *HORDEUM PUSILLUM, H. VULGARE, KOELERIA MACRANTHA* and *Leersia oryzoides.*

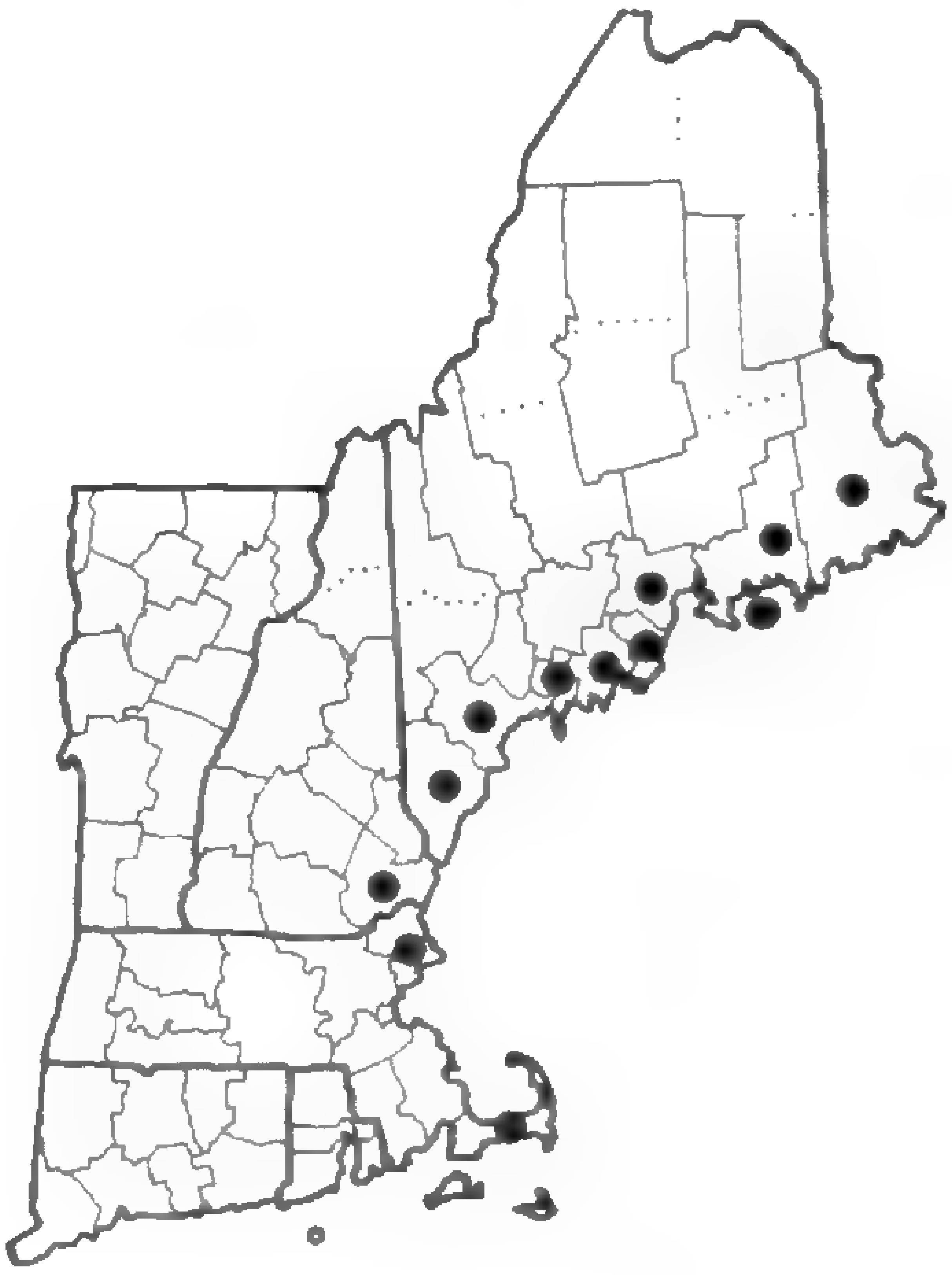


Leersia virginica



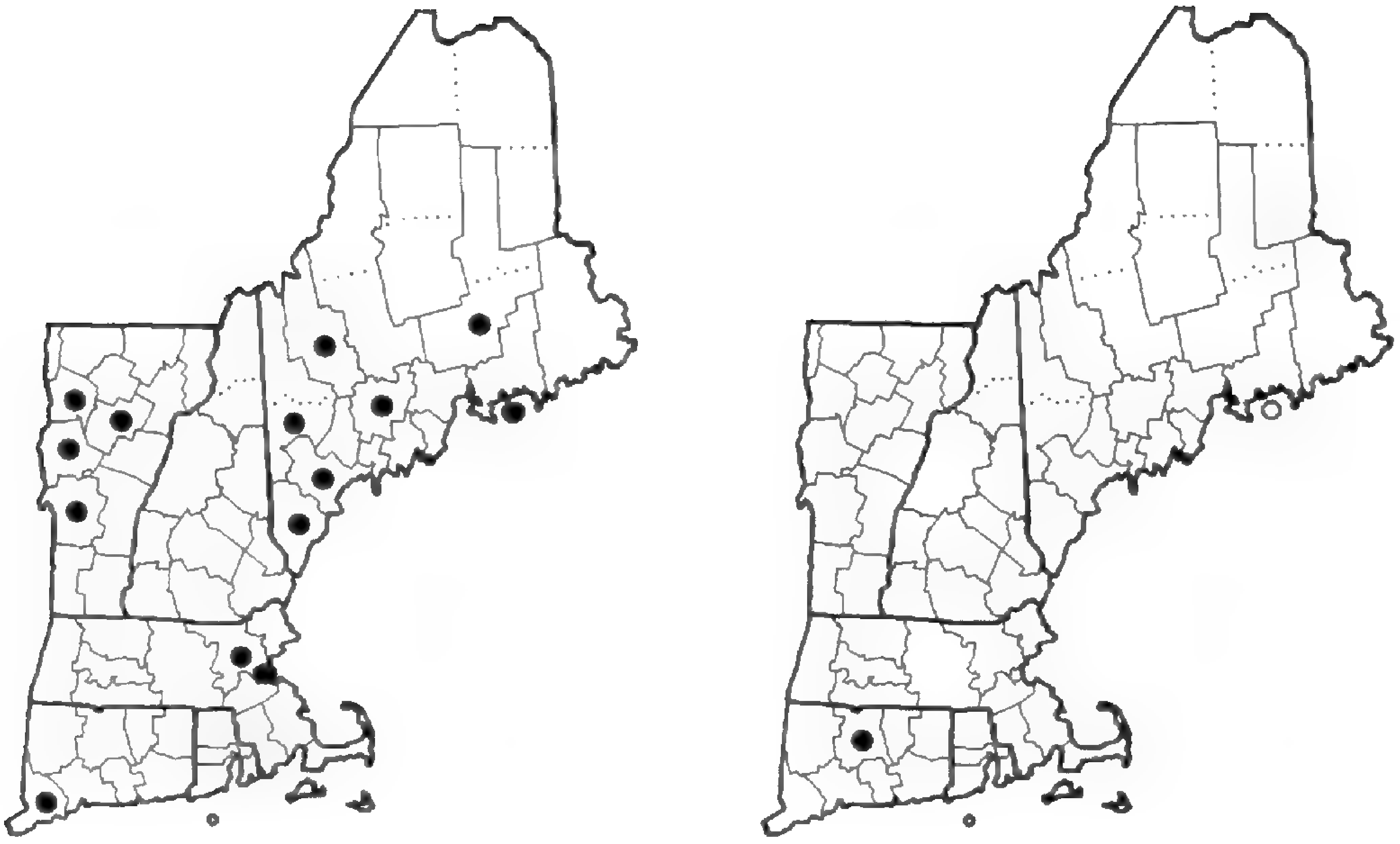
Leptochloa fascicularis

LEPTOCHLOA PANICEA subsp. *MUCRONATA*

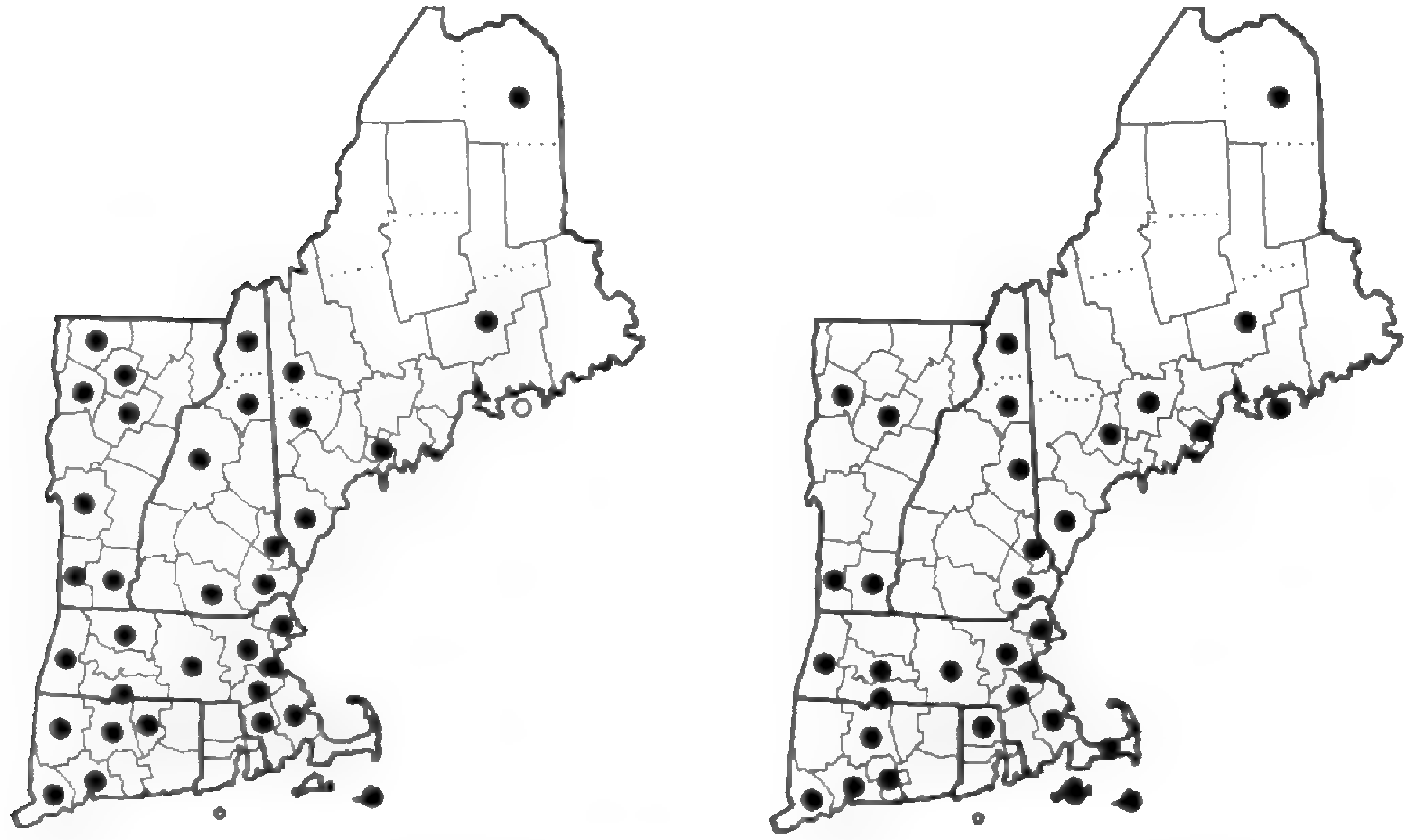


Leymus mollis

Figure 46. Distribution maps for *Leersia virginica, Leptochloa fascicularis, L. PANICEA* subsp. *MUCRONATA* and *Leymus mollis*.

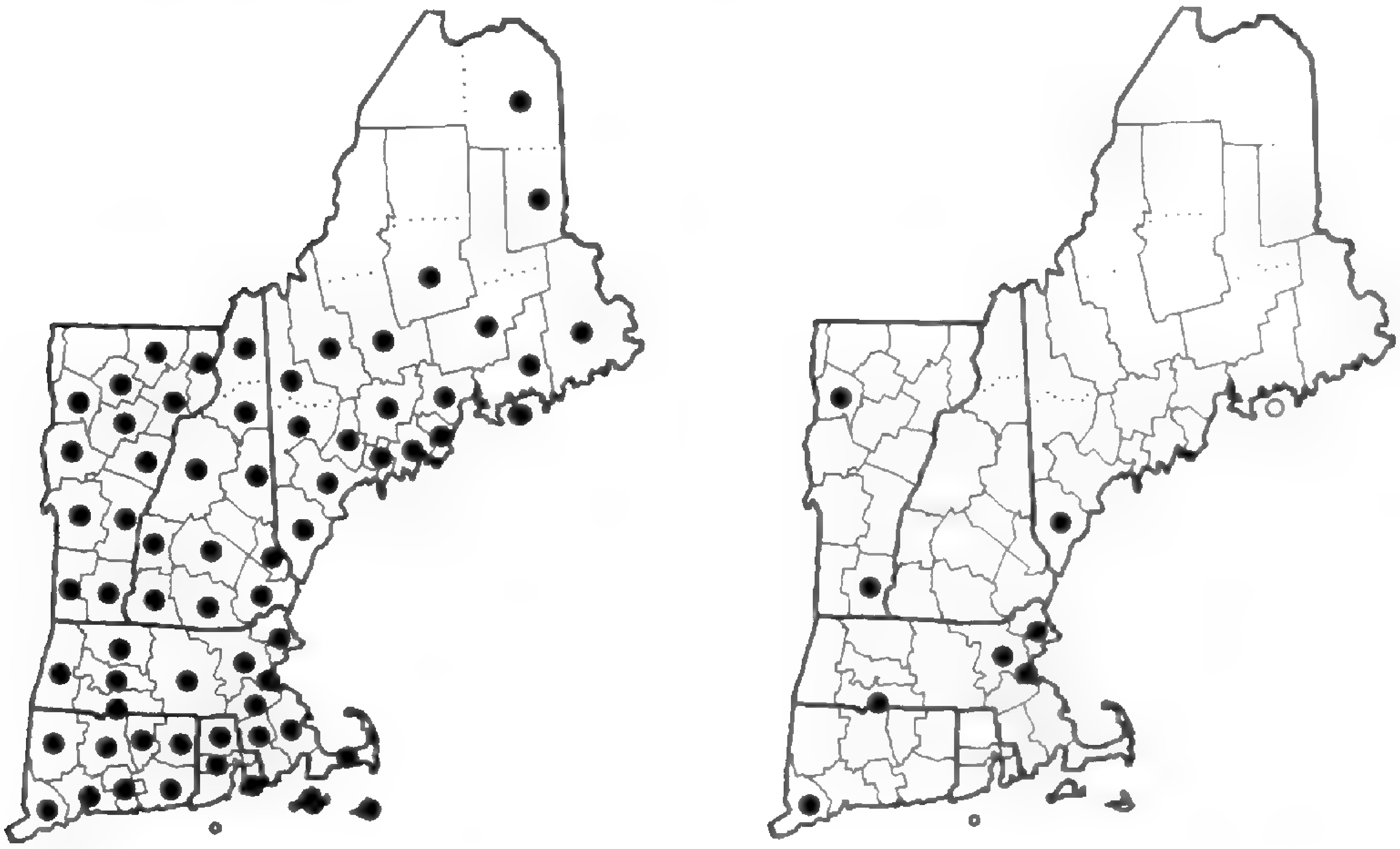


LOLIUM ARUNDINACEUM *LOLIUM GIGANTEUM*



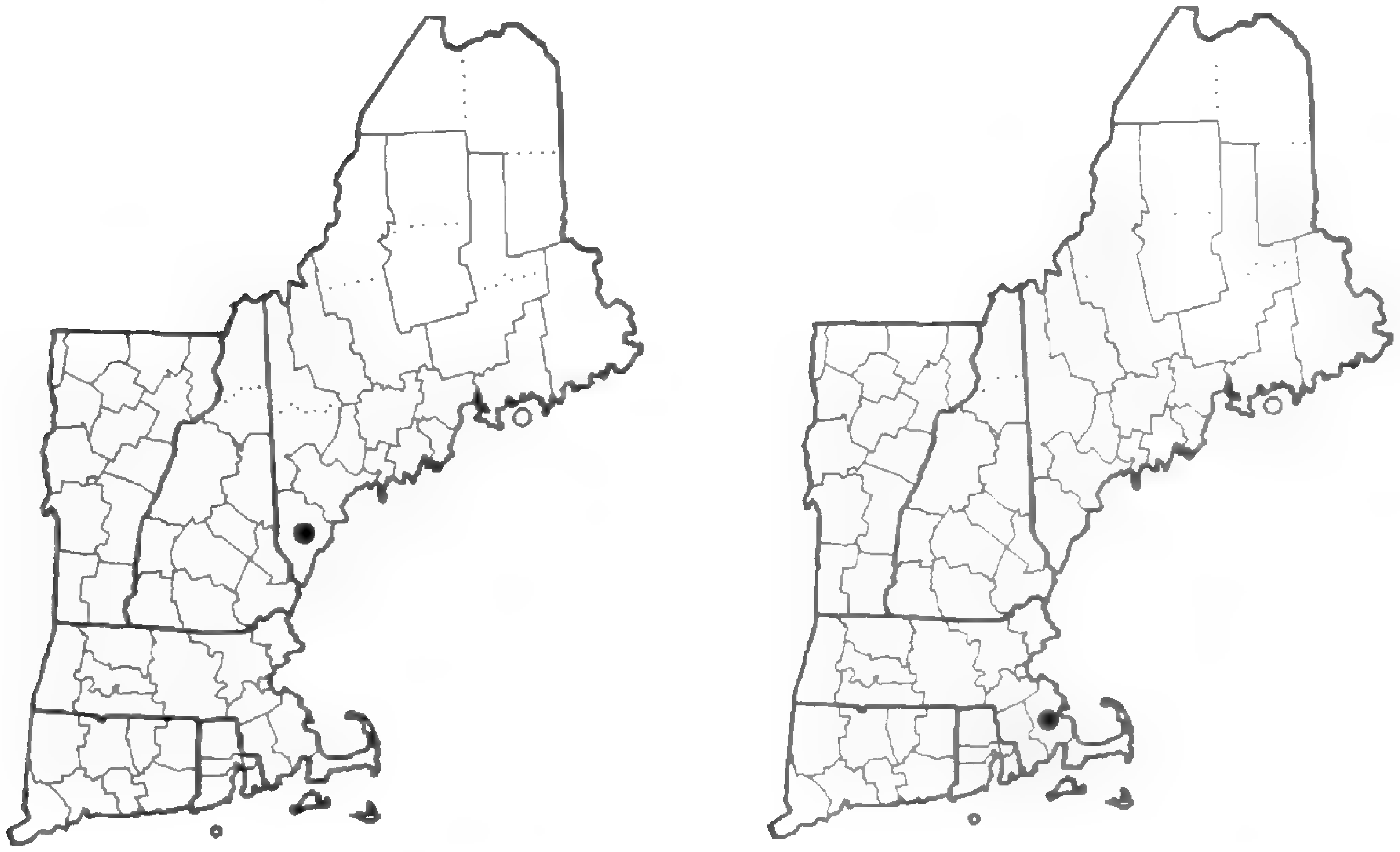
LOLIUM MULTIFLORUM *LOLIUM PERENNE*

Figure 47. Distribution maps for *LOLIUM ARUNDINACEUM, L. GIGANTEUM, L. MULTIFLORUM* and *L. PERENNE.*



LOLIUM PRATENSE

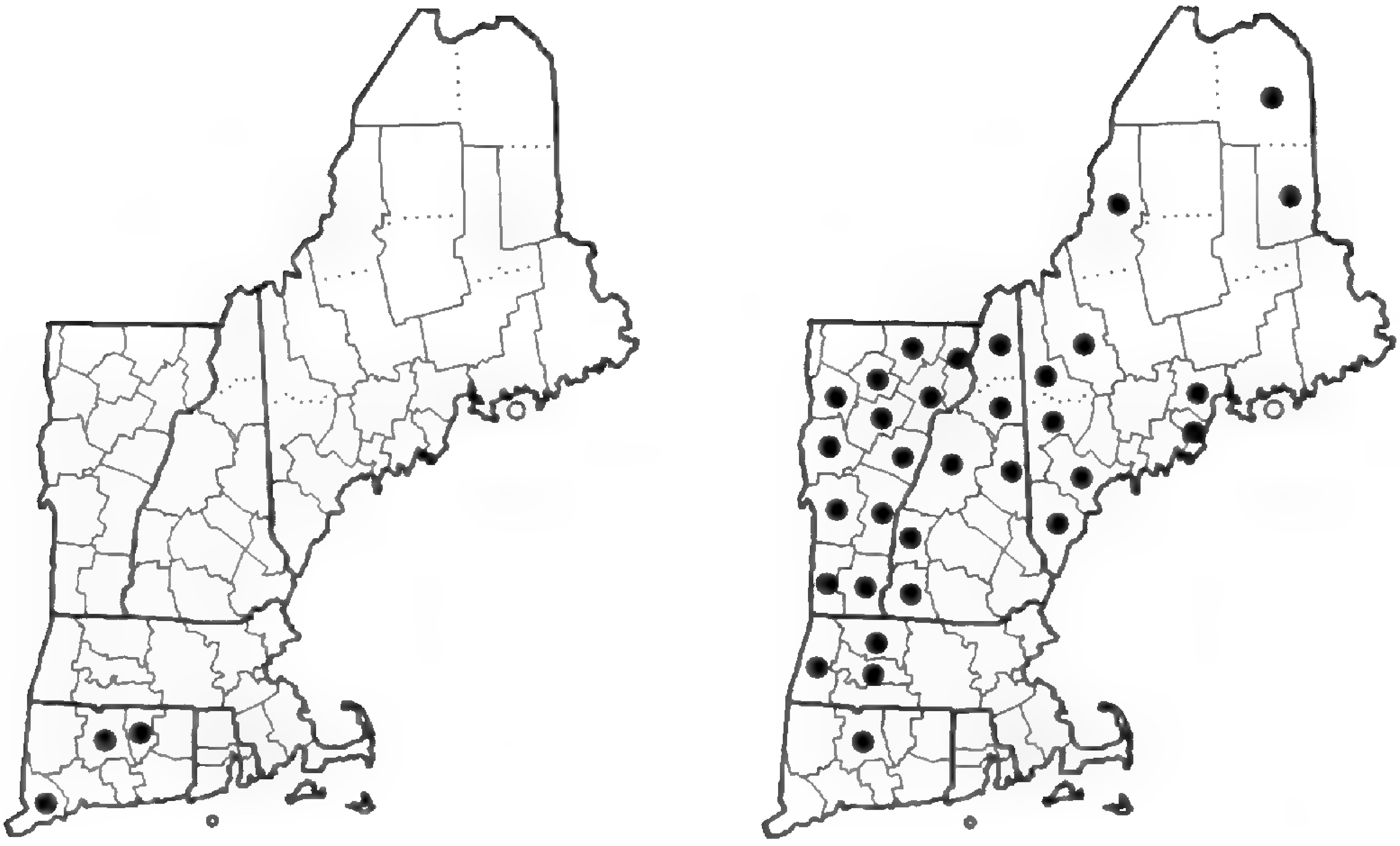
LOLIUM TEMULENTUM



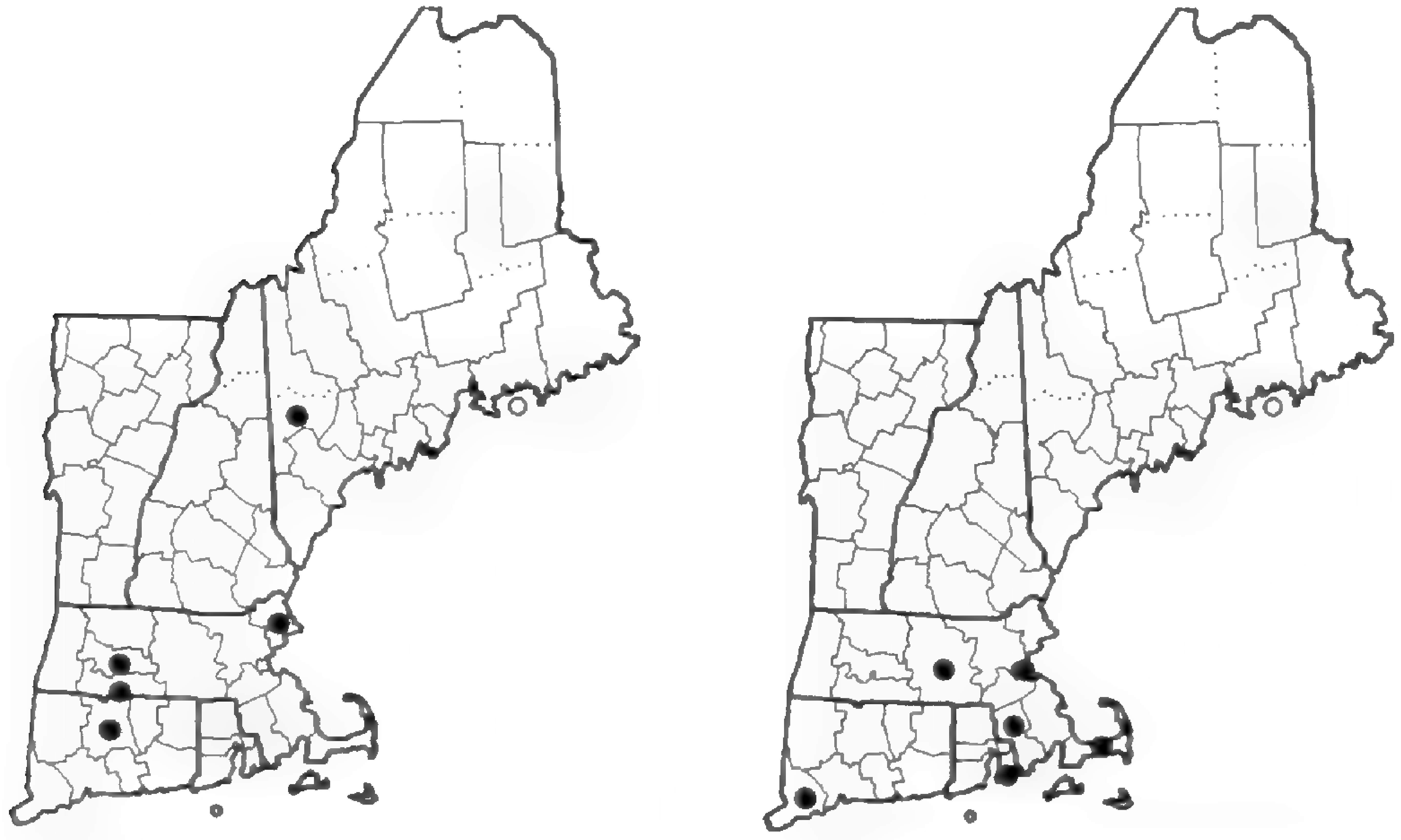
LYCURUS PHLEOIDES

MIBORA MINIMA

Figure 48. Distribution maps for *LOLIUM PRATENSE, L. TEMULENTUM, LYCURUS PHLEOIDES* and *MIBORA MINIMA*.

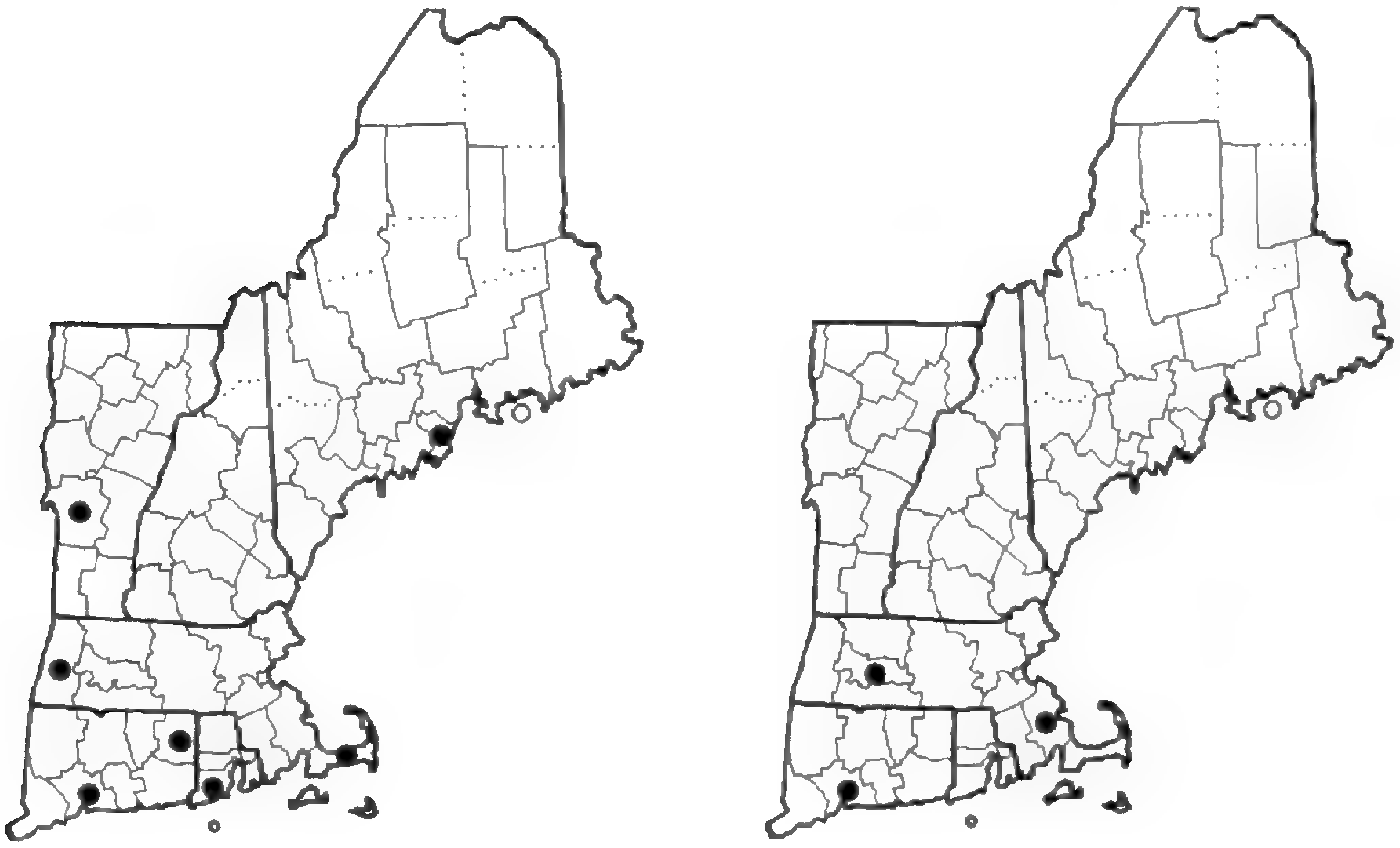


MICROSTEGIUM VIMINEUM　　*Milium effusum*

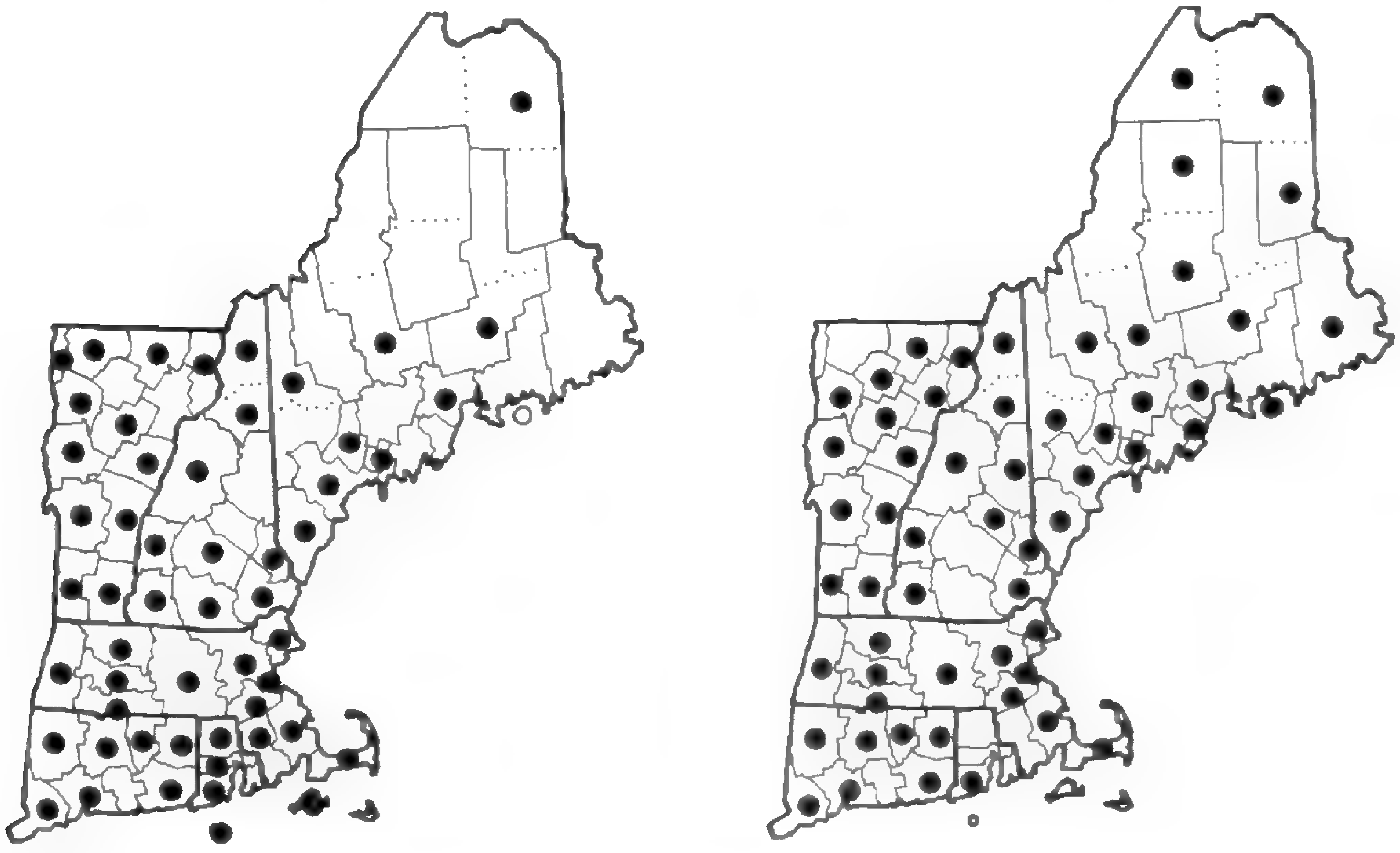


MISCANTHUS SACCHARIFLORUS　　*MISCANTHUS SINENSIS*

Figure 49. Distribution maps for *MICROSTEGIUM VIMINEUM*, *Milium effusum*, *MISCANTHUS SACCHARIFLORUS* and *M. SINENSIS*.

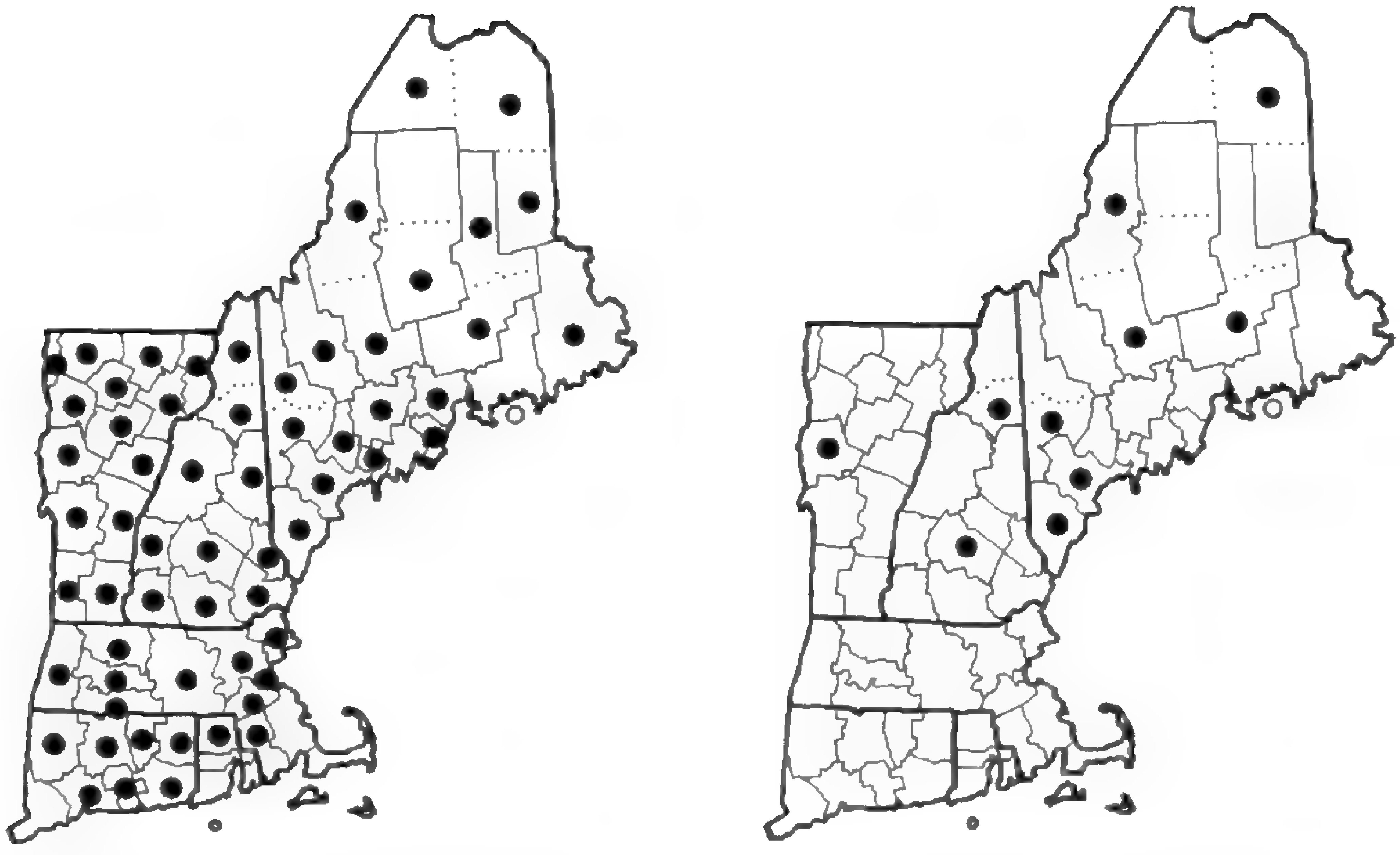


MOLINIA CAERULEA *Muhlenbergia capillaris*



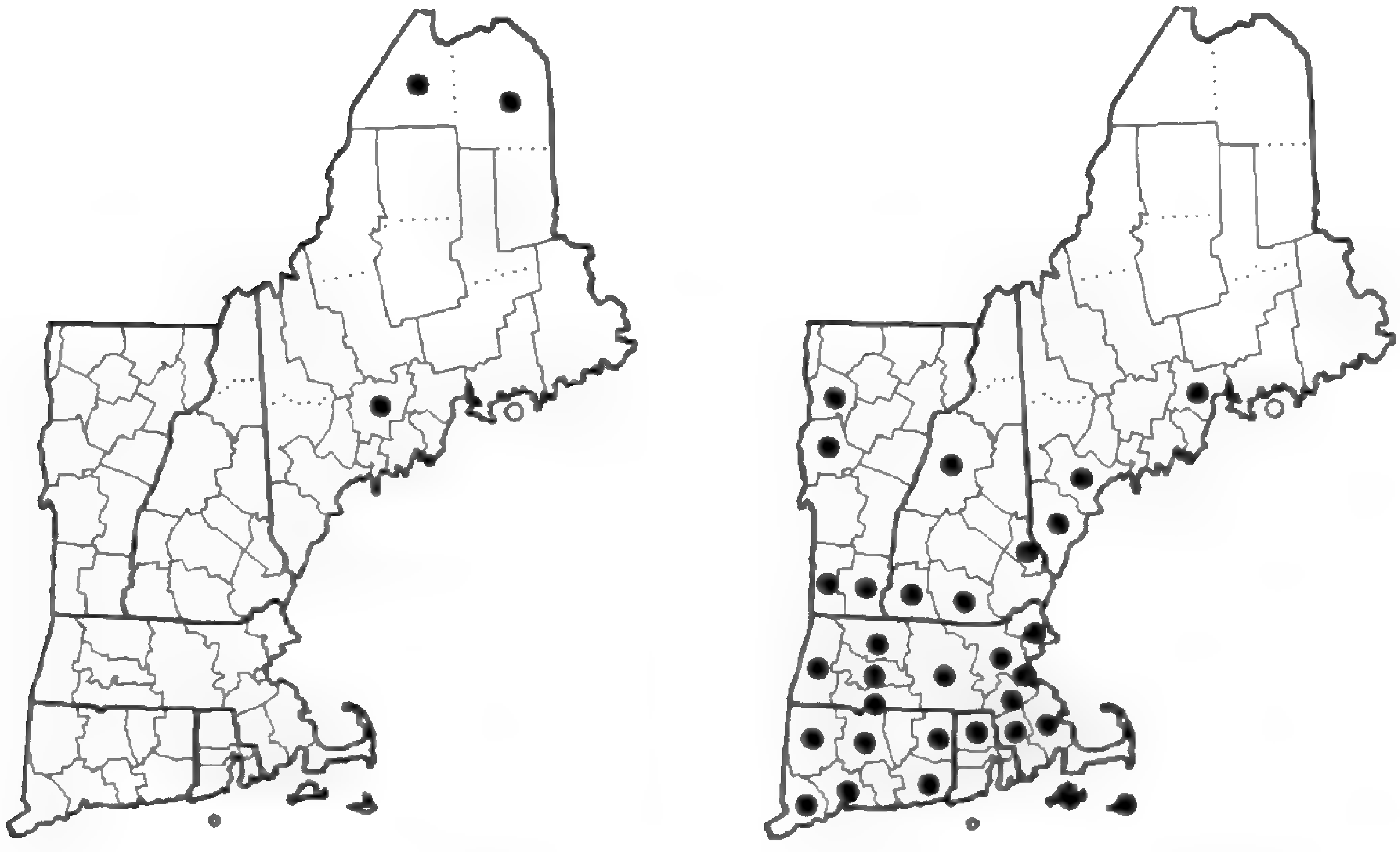
Muhlenbergia frondosa *Muhlenbergia glomerata*

Figure 50. Distribution maps for *MOLINIA CAERULEA*, *Muhlenbergia capillaris*, *M. frondosa* and *M. glomerata*.



Muhlenbergia mexicana

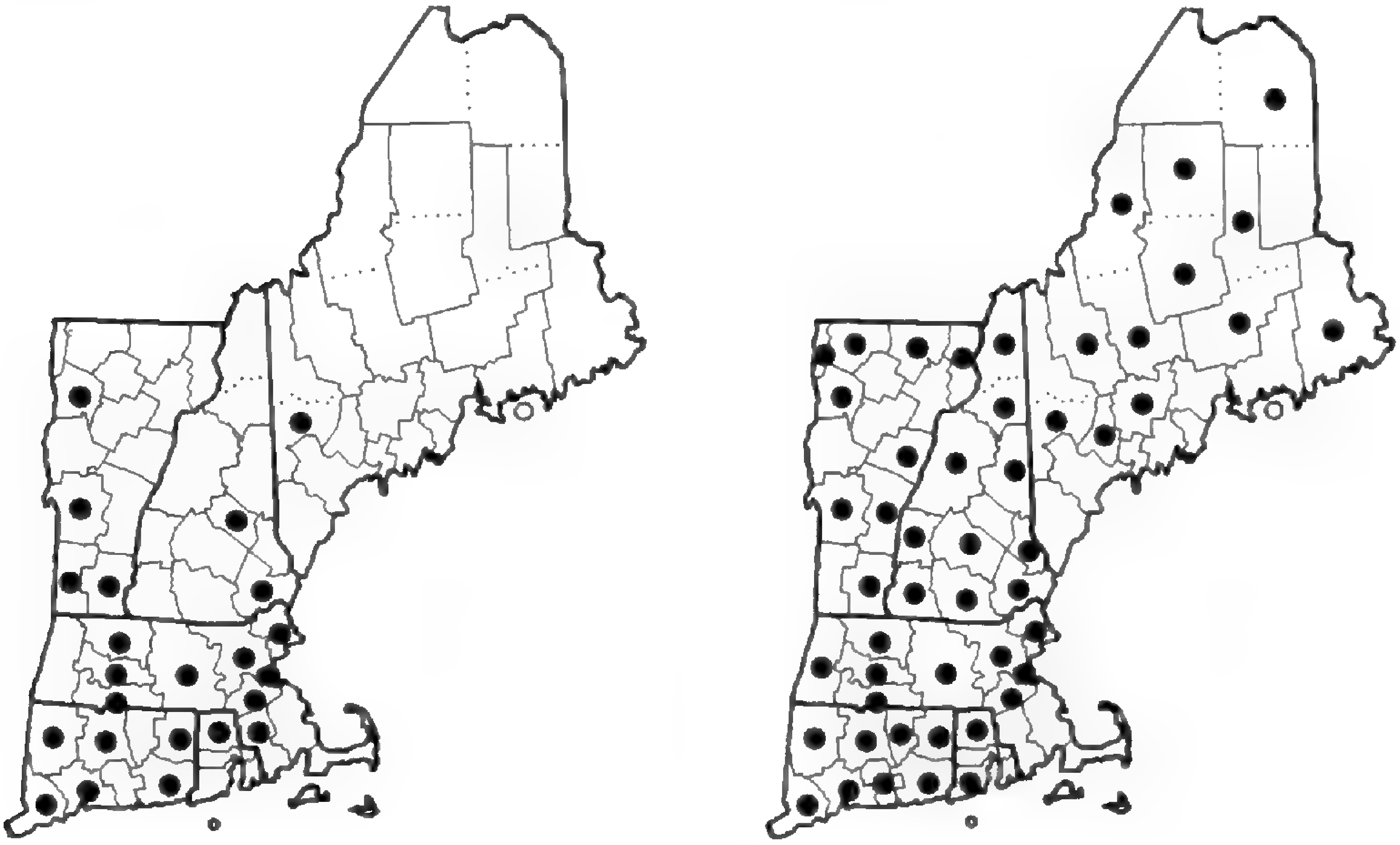
MUHLENBERGIA RACEMOSA



Muhlenbergia richardsonis

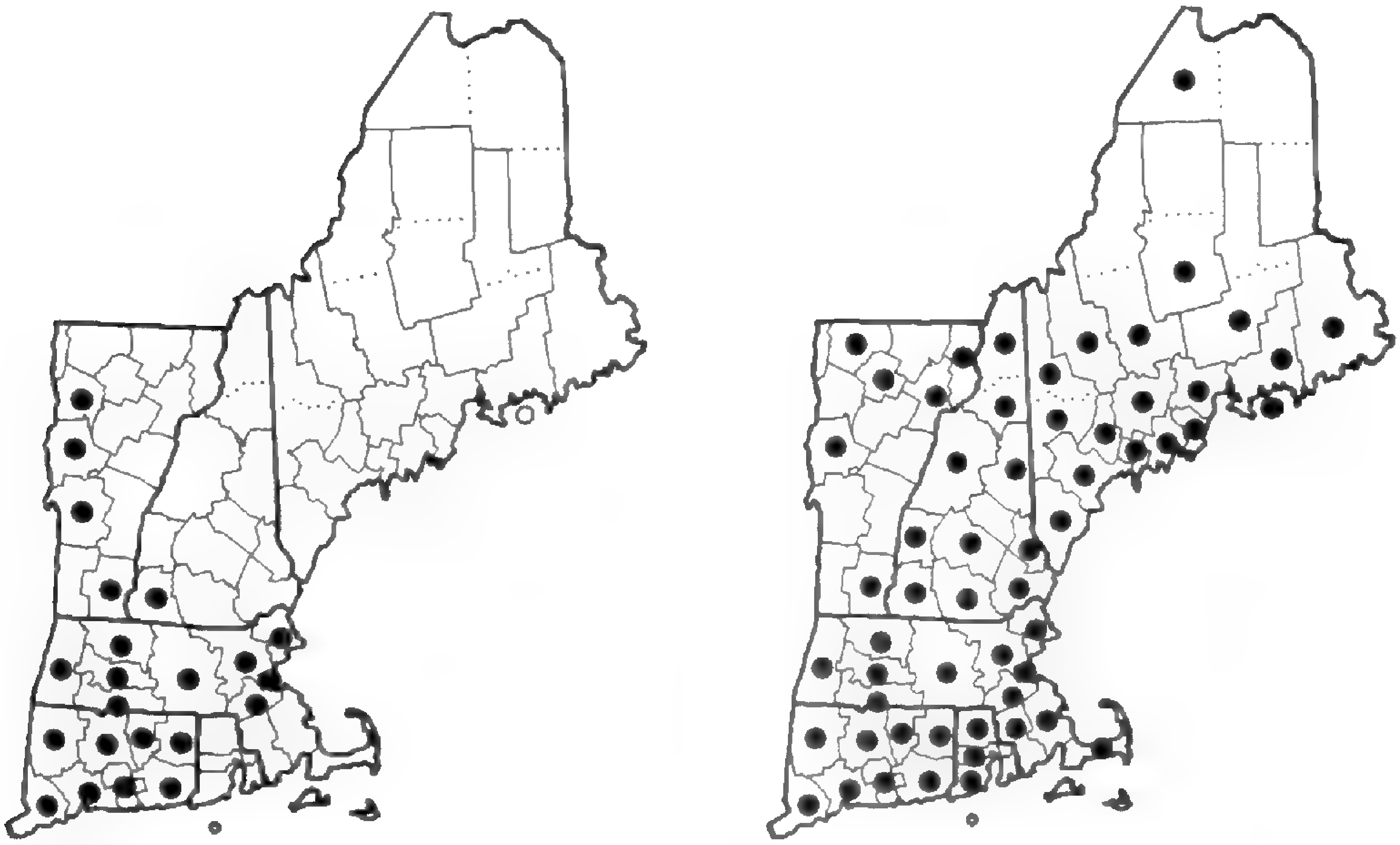
Muhlenbergia schreberi

Figure 51. Distribution maps for *Muhlenbergia mexicana, M. RACEMOSA, M. richardsonis* and *M. schreberi.*



Muhlenbergia sobolifera

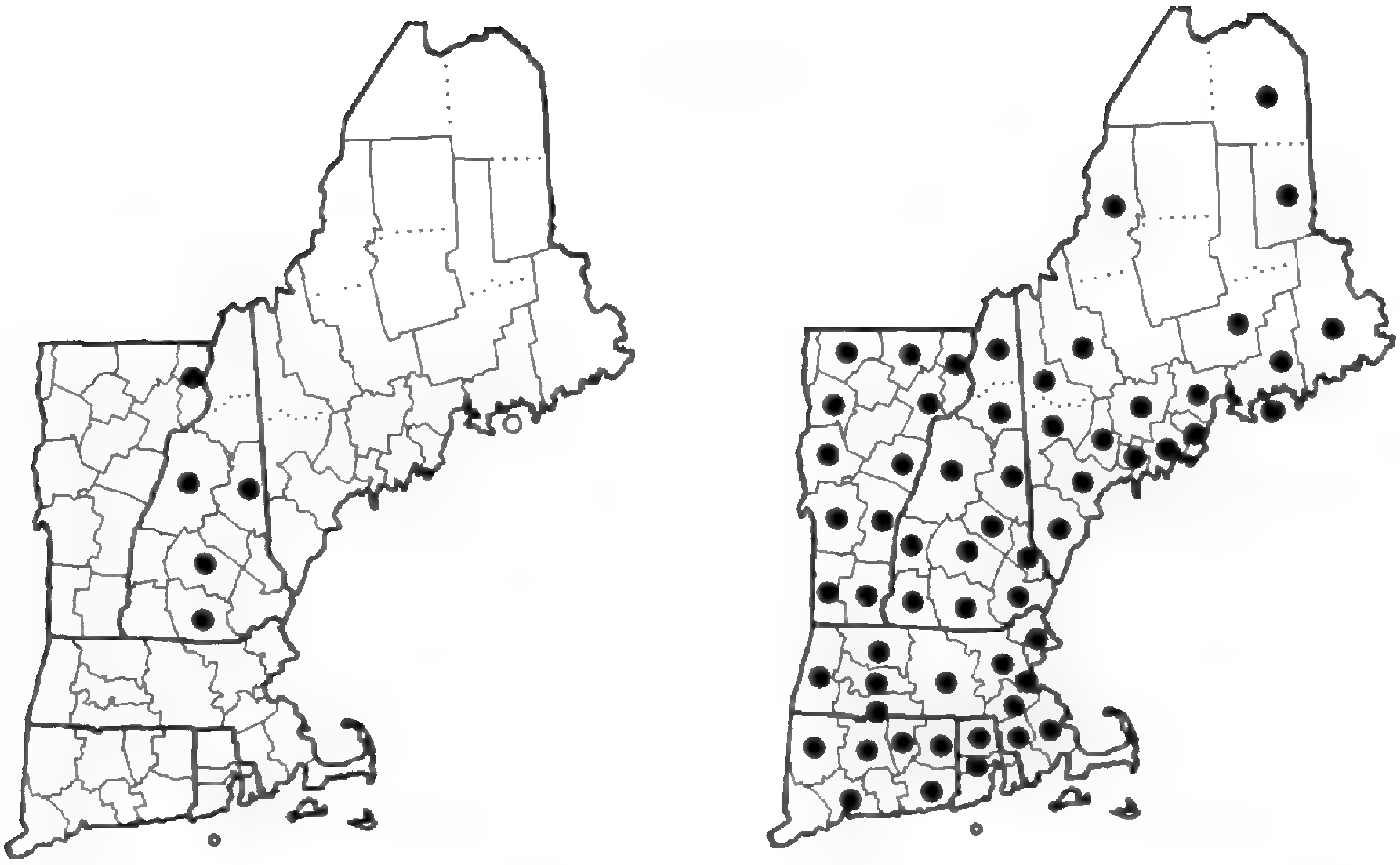
Muhlenbergia sylvatica



Muhlenbergia tenuiflora

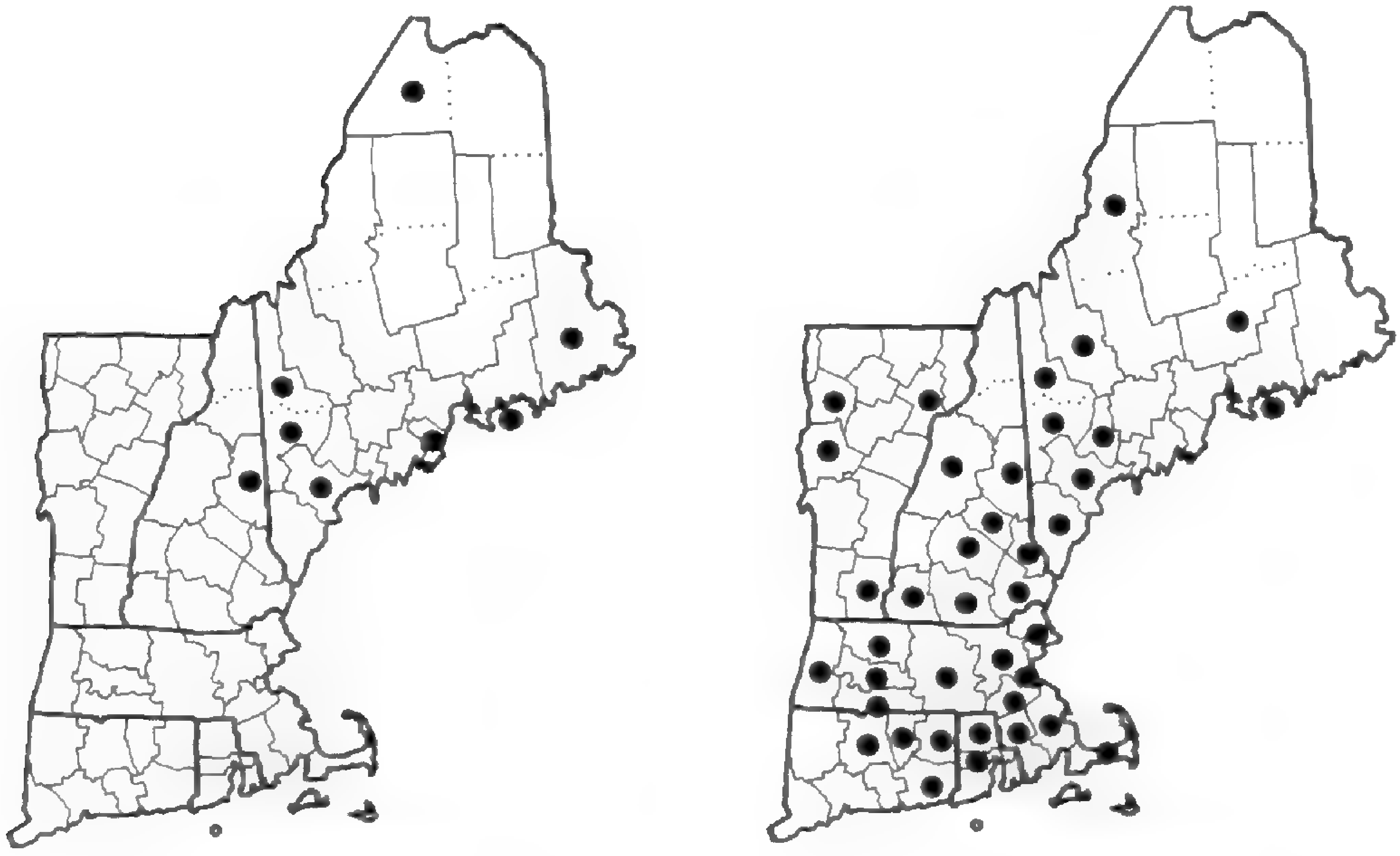
Muhlenbergia uniflora

Figure 52. Distribution maps for *Muhlenbergia sobolifera*, *M. sylvatica*, *M. tenuiflora* and *M. uniflora*.



NARDUS STRICTA

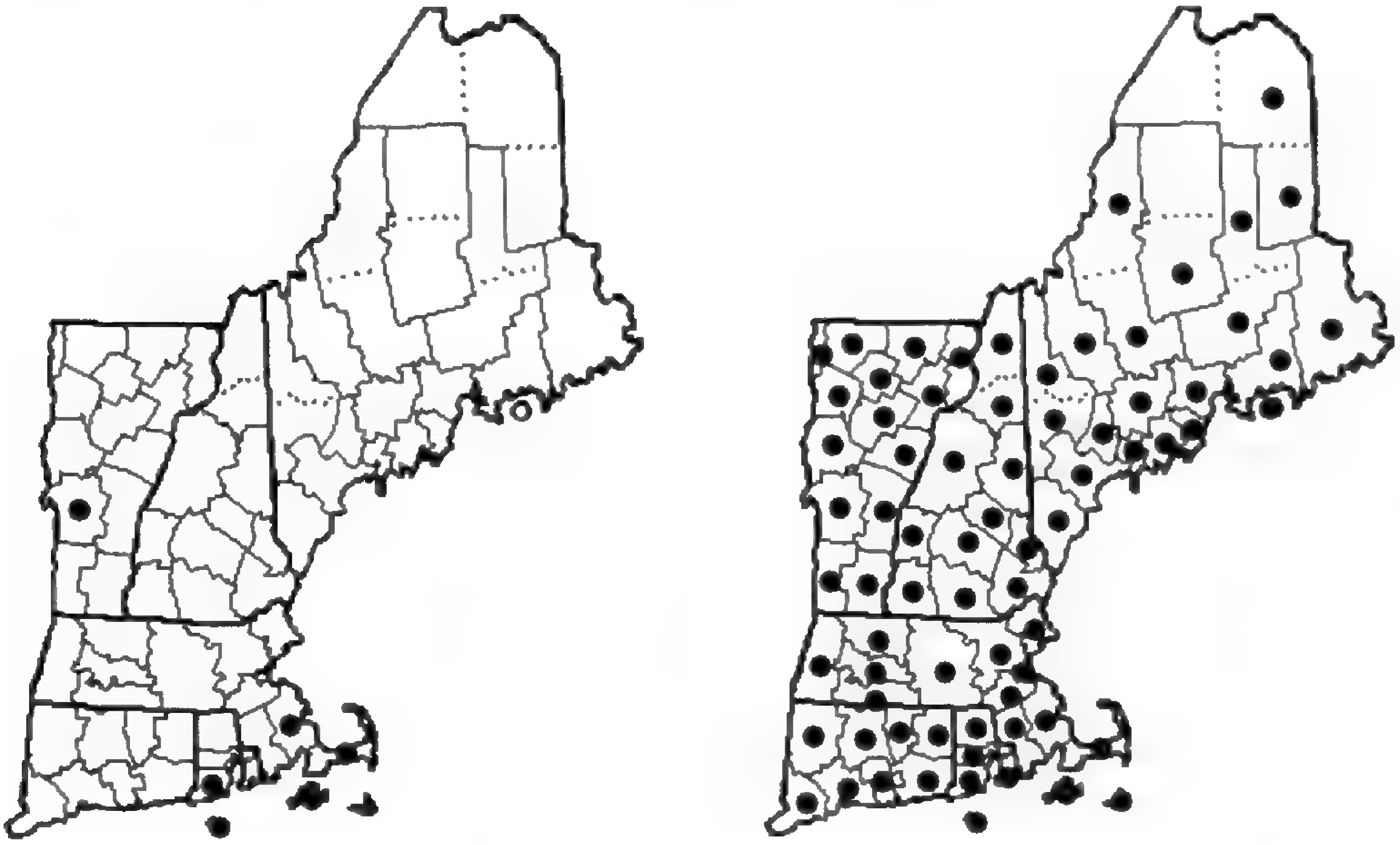
Oryzopsis asperifolia



Oryzopsis canadensis

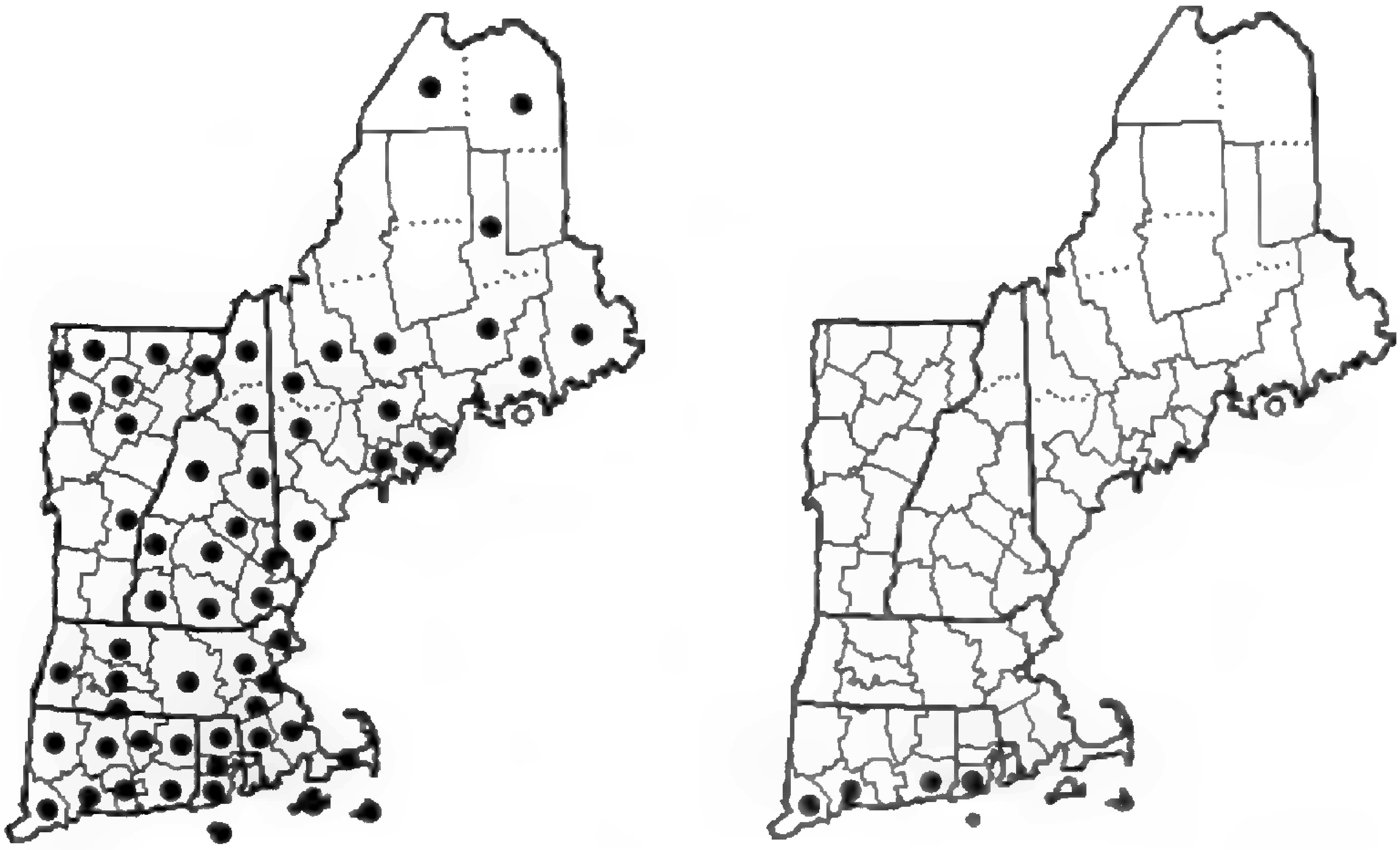
Oryzopsis pungens

Figure 53. Distribution maps for *NARDUS STRICTA*, *Oryzopsis asperifolia*, *O. canadensis* and *O. pungens*.



Panicum acuminatum var. *acuminatum*

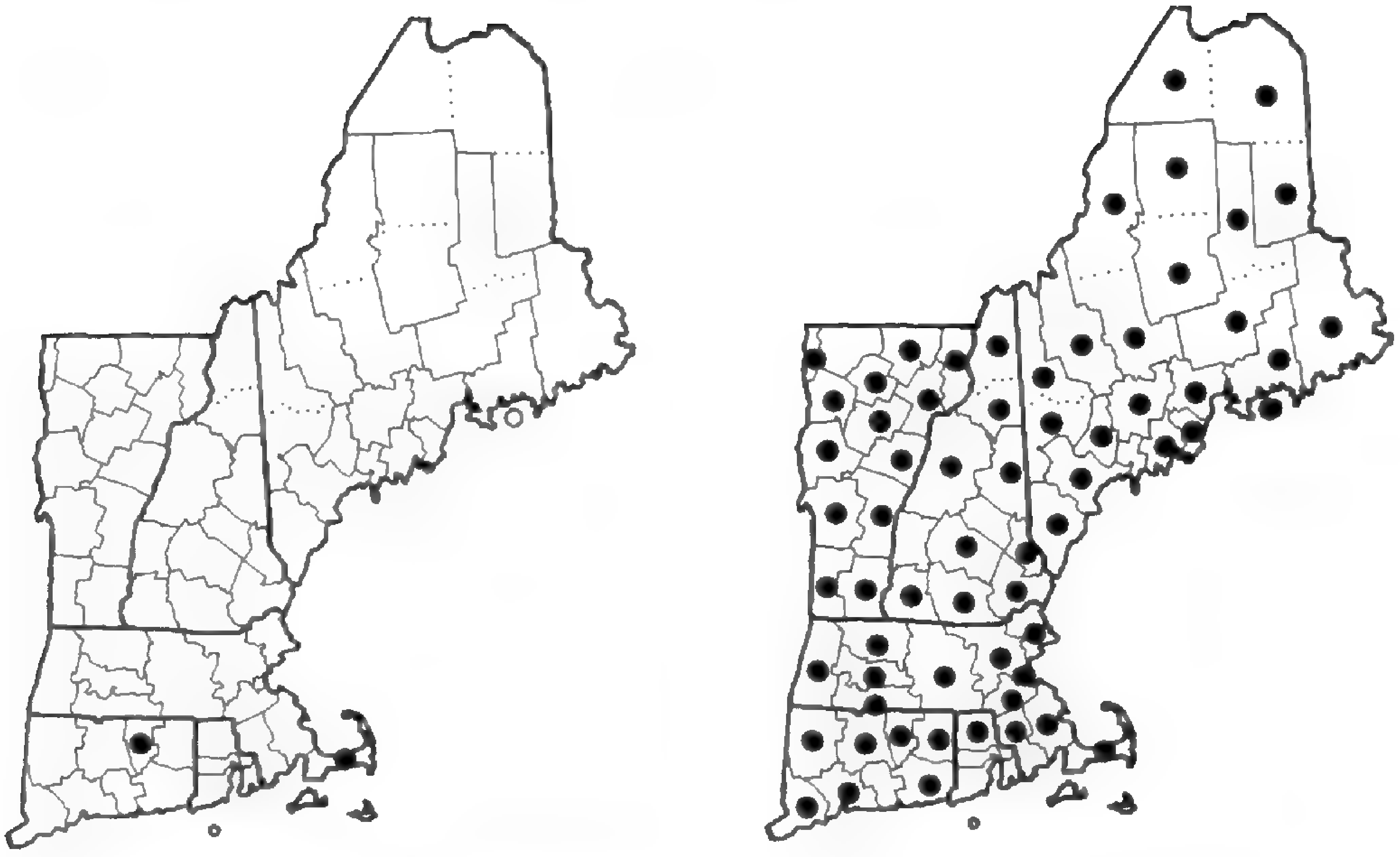
Panicum acuminatum var. *fasciculatum*



Panicum acuminatum var. *lindheimeri*

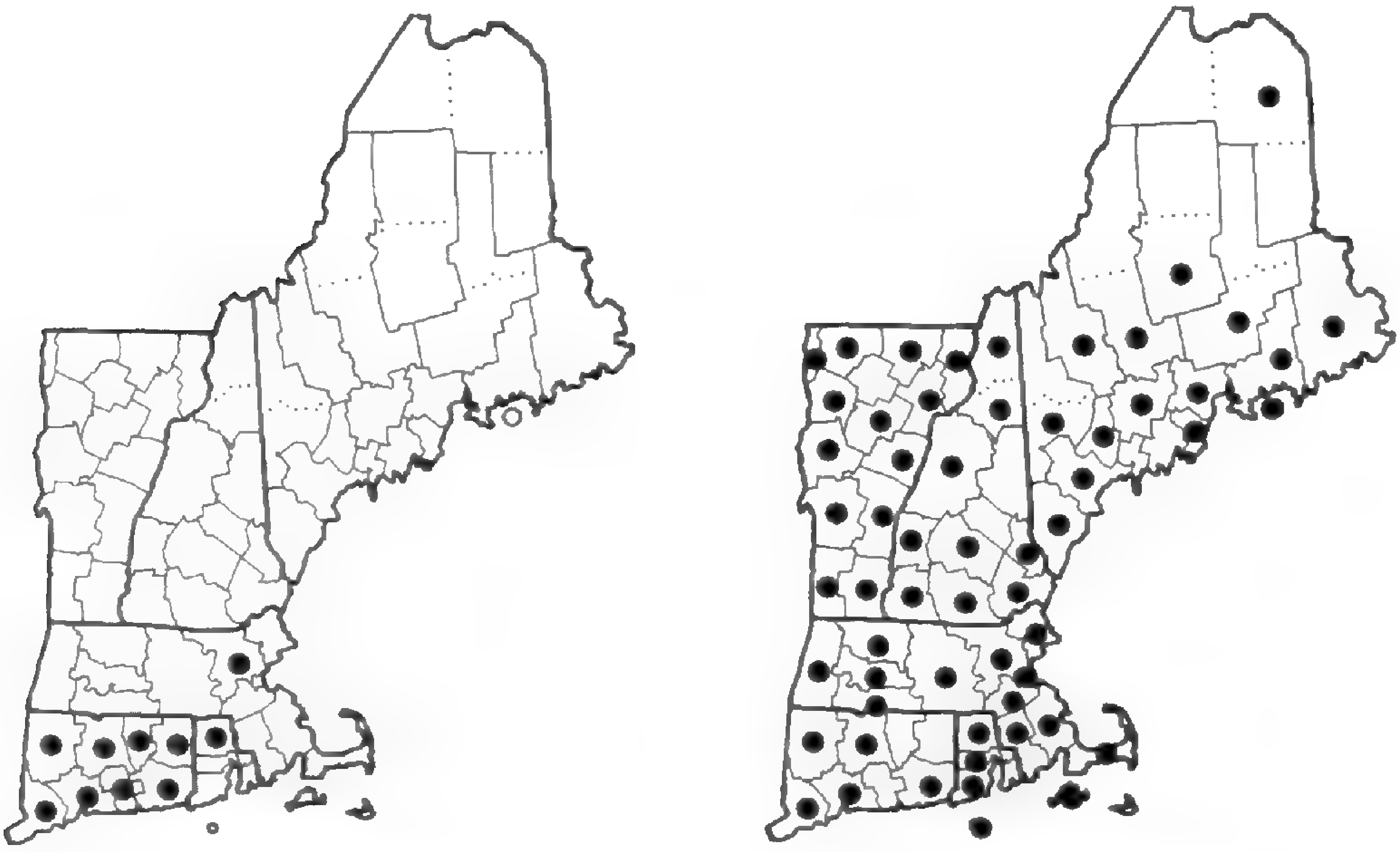
Panicum amarum var. *amarum*

Figure 54. Distribution maps for *Panicum acuminatum* var. *acuminatum*, *P. acuminatum* var. *fasciculatum*, *P. acuminatum* var. *lindheimeri* and *P. amarum* var. *amarum*.



Panicum amarum var. *amarulum*

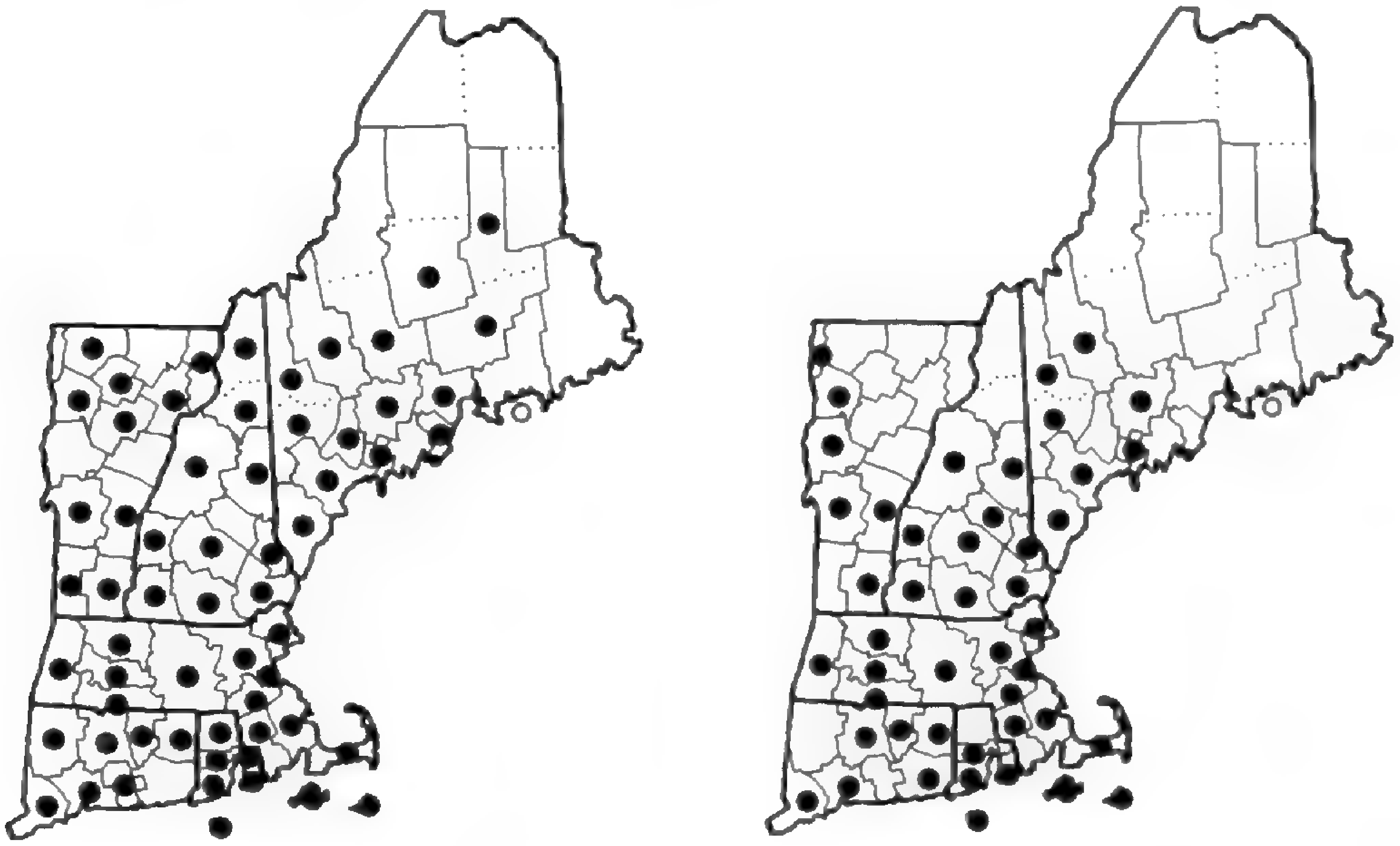
Panicum boreale



Panicum boscii

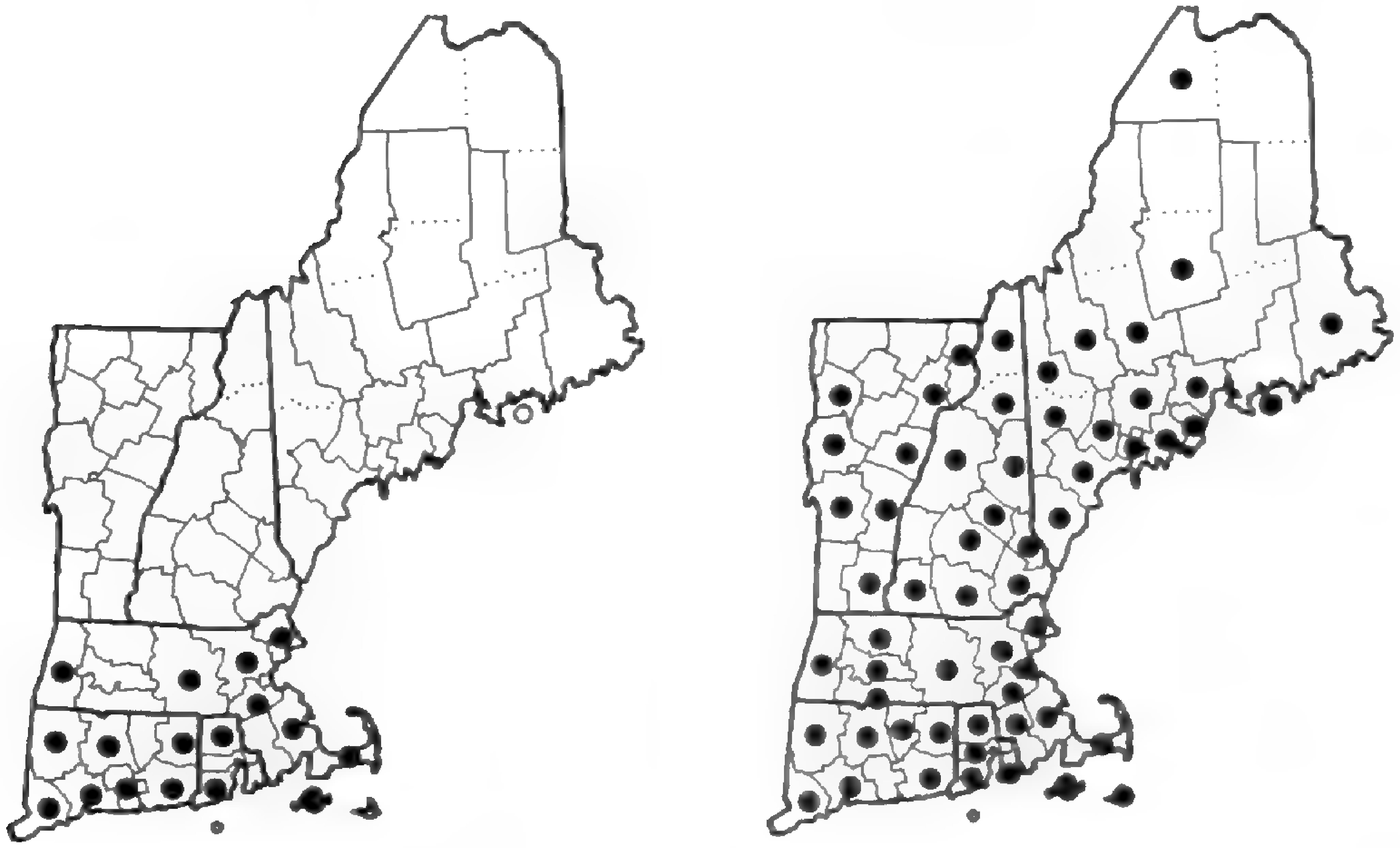
Panicum capillare

Figure 55. Distribution maps for *Panicum amarum* var. *amarulum*, *P. boreale*, *P. boscii* and *P. capillare*.



Panicum clandestinum

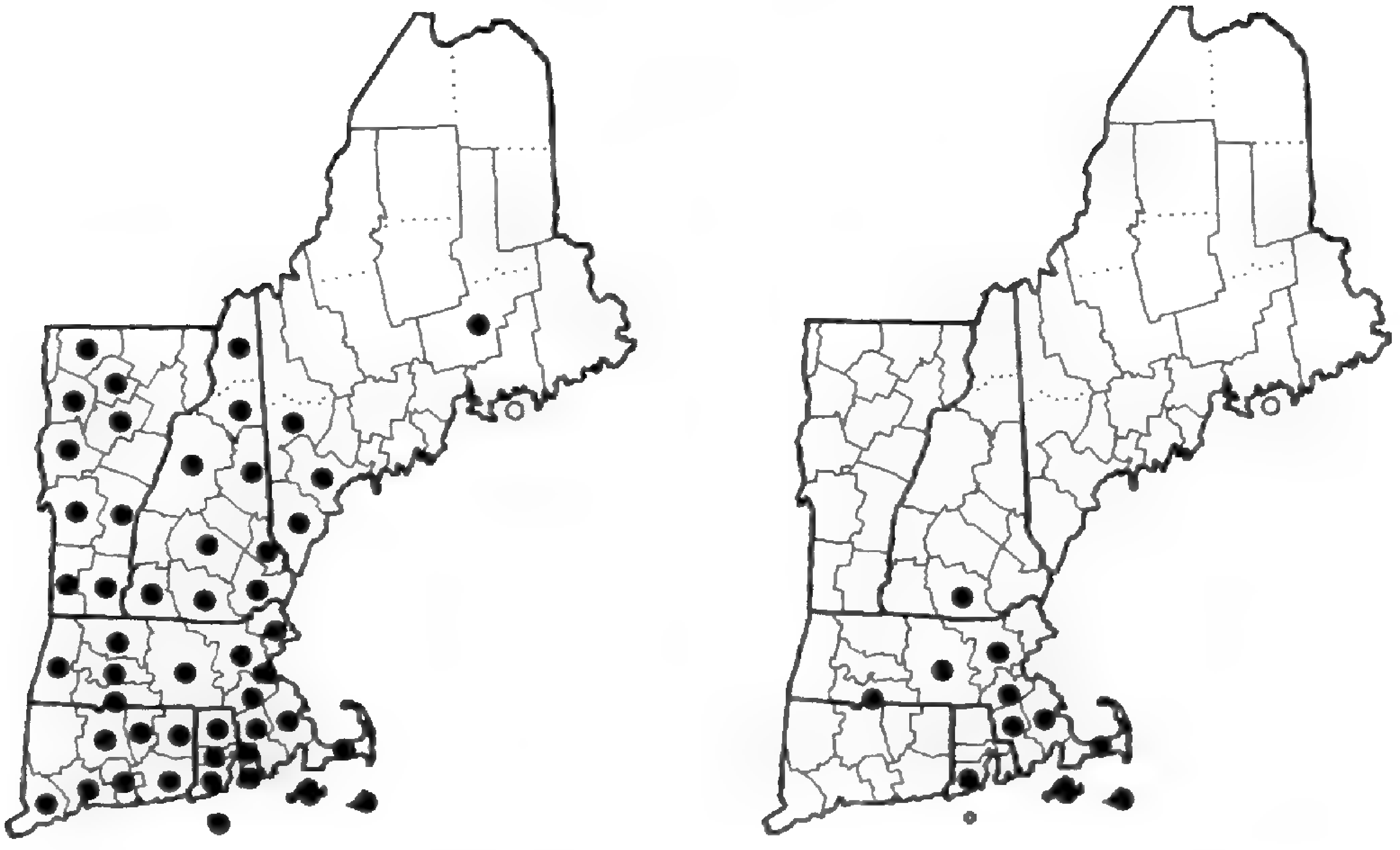
Panicum columbianum



Panicum commutatum var. *ashei*

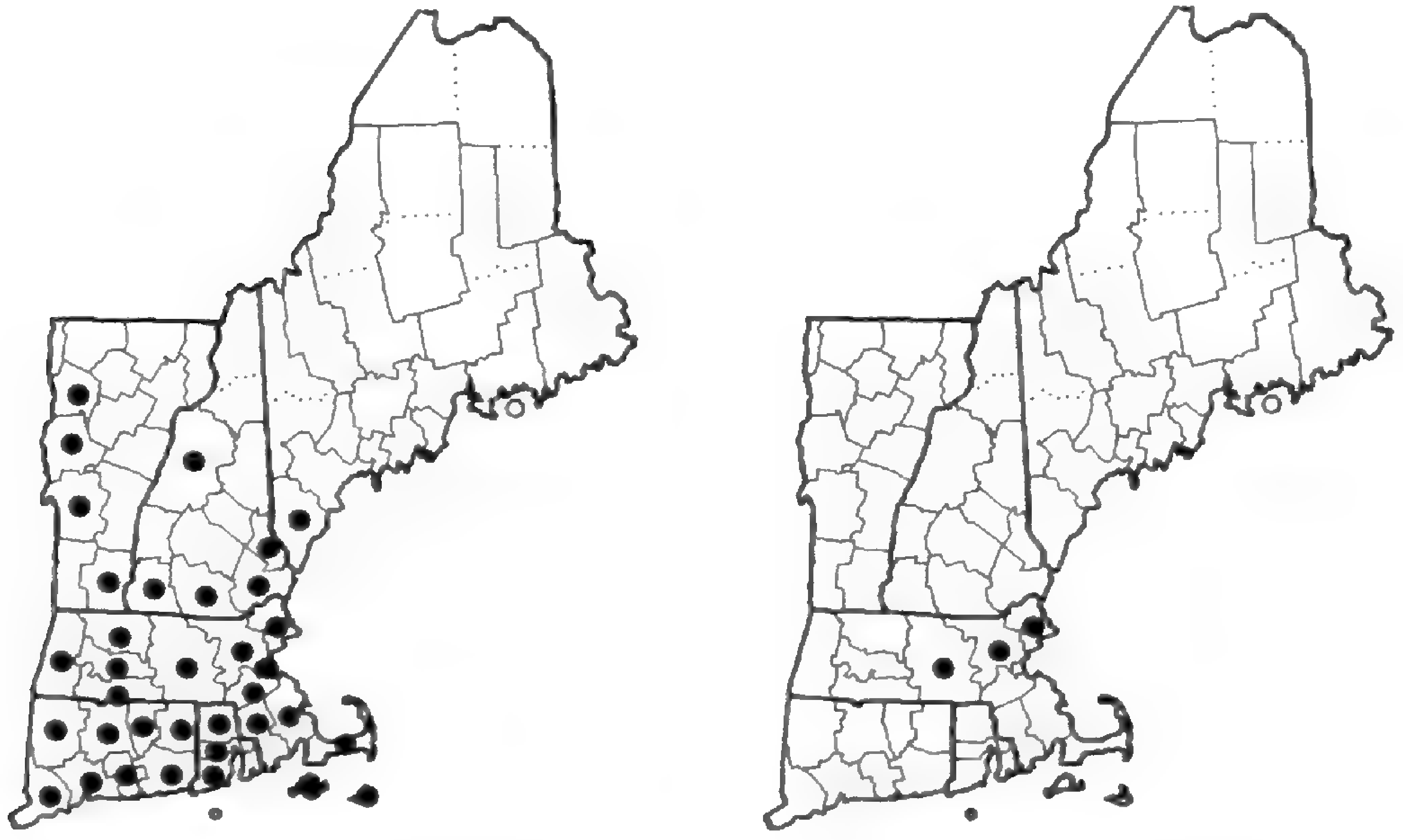
Panicum depauperatum

Figure 56. Distribution maps for *Panicum clandestinum, P. columbianum, P. commutatum* var. *ashei* and *P. depauperatum.*



Panicum dichotomiflorum
var. *dichotomiflorum*

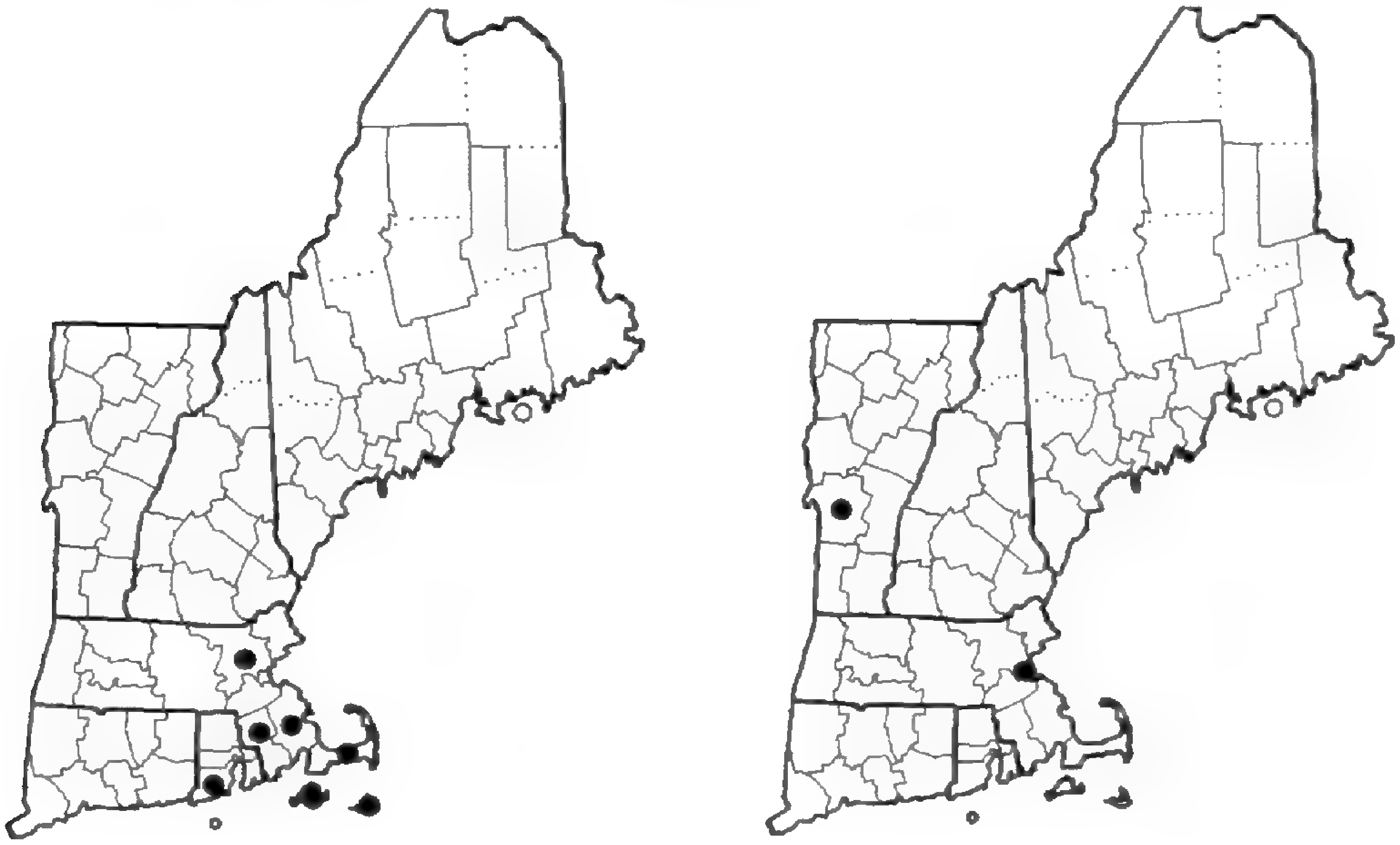
Panicum dichotomiflorum
var. *puritanorum*



Panicum dichotomum
var. *dichotomum*

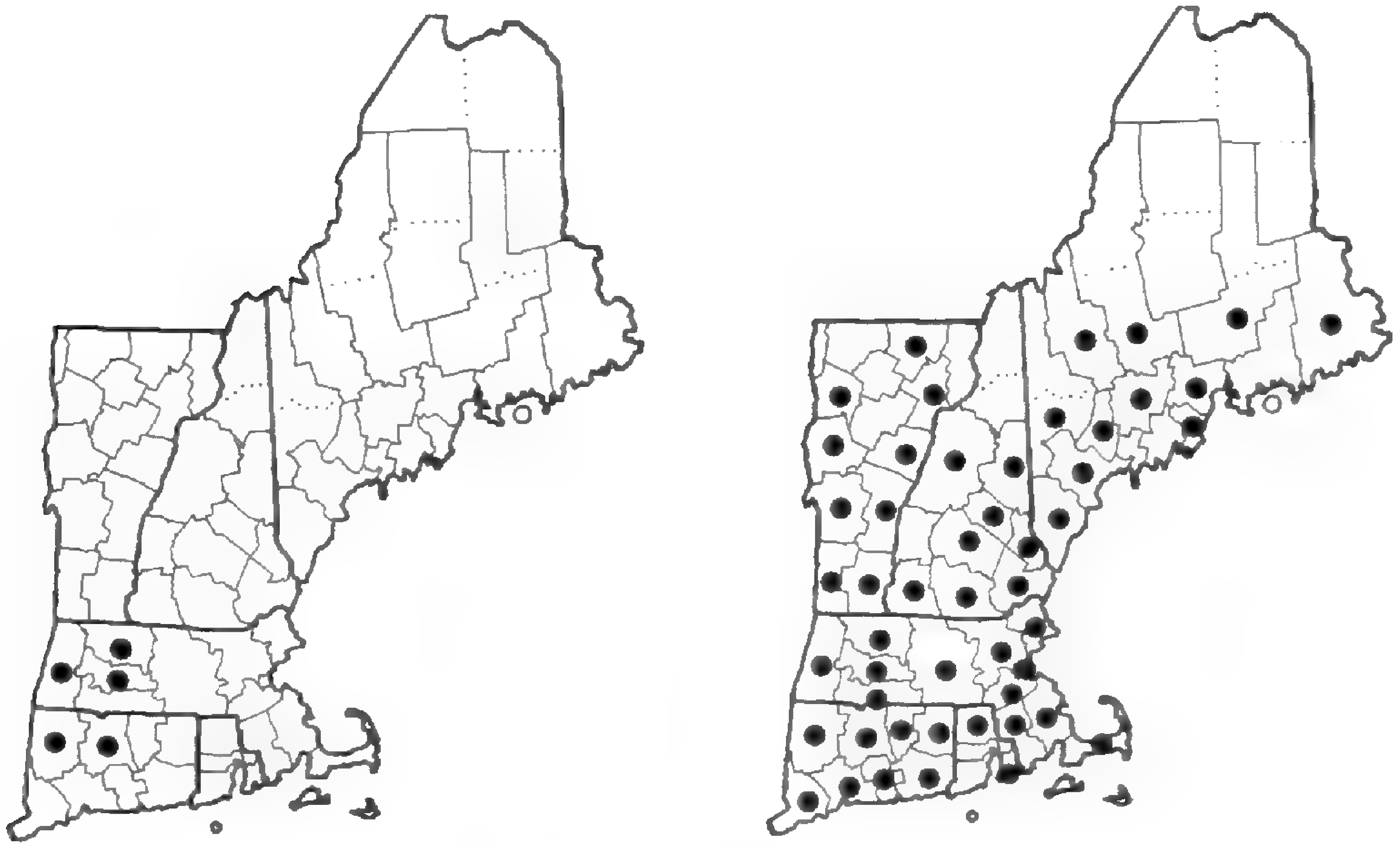
Panicum dichotomum
var. *lucidum*

Figure 57. Distribution maps for *Panicum dichotomiflorum* var. *dichotomiflorum, P. dichotomiflorum* var. *puritanorum, P. dichotomum* var. *dichotomum* and *P. dichotomum* var. *lucidum.*



Panicum dichotomum var. mattamuskeetense

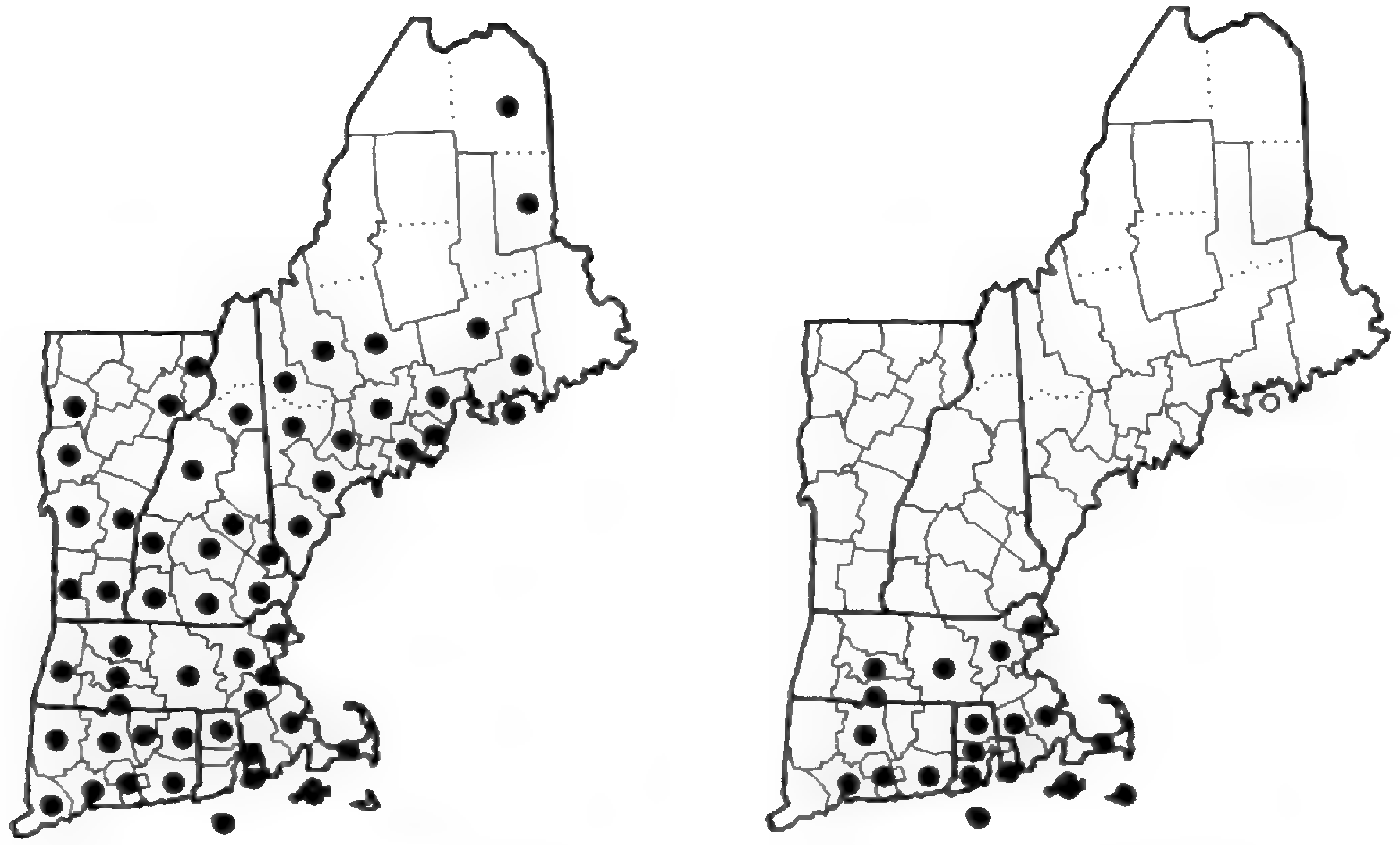
Panicum flexile



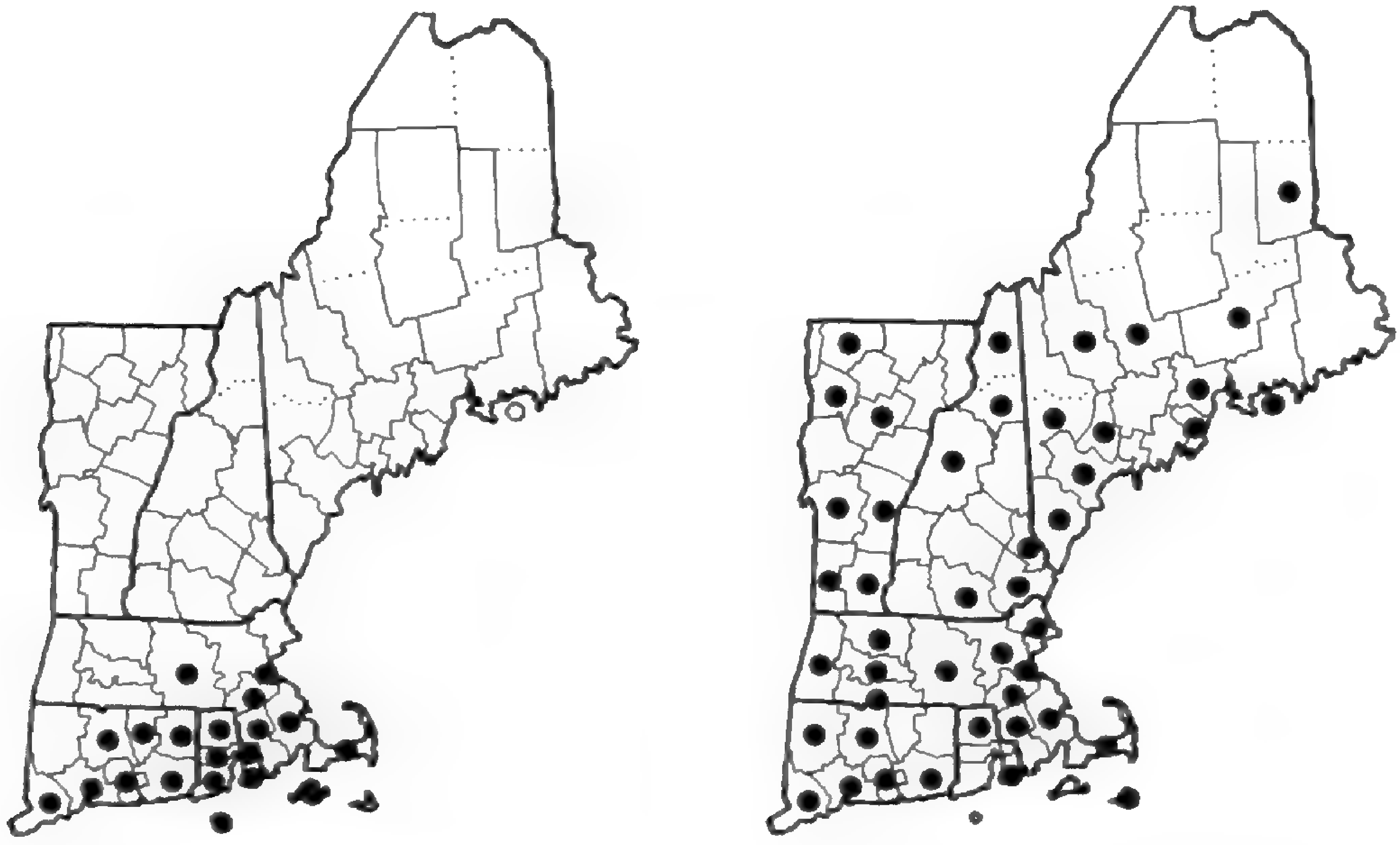
Panicum gattingeri

Panicum latifolium

Figure 58. Distribution maps for *Panicum dichotomum* var. *mattamuskeetense, P. flexile, P. gattingeri* and *P. latifolium.*

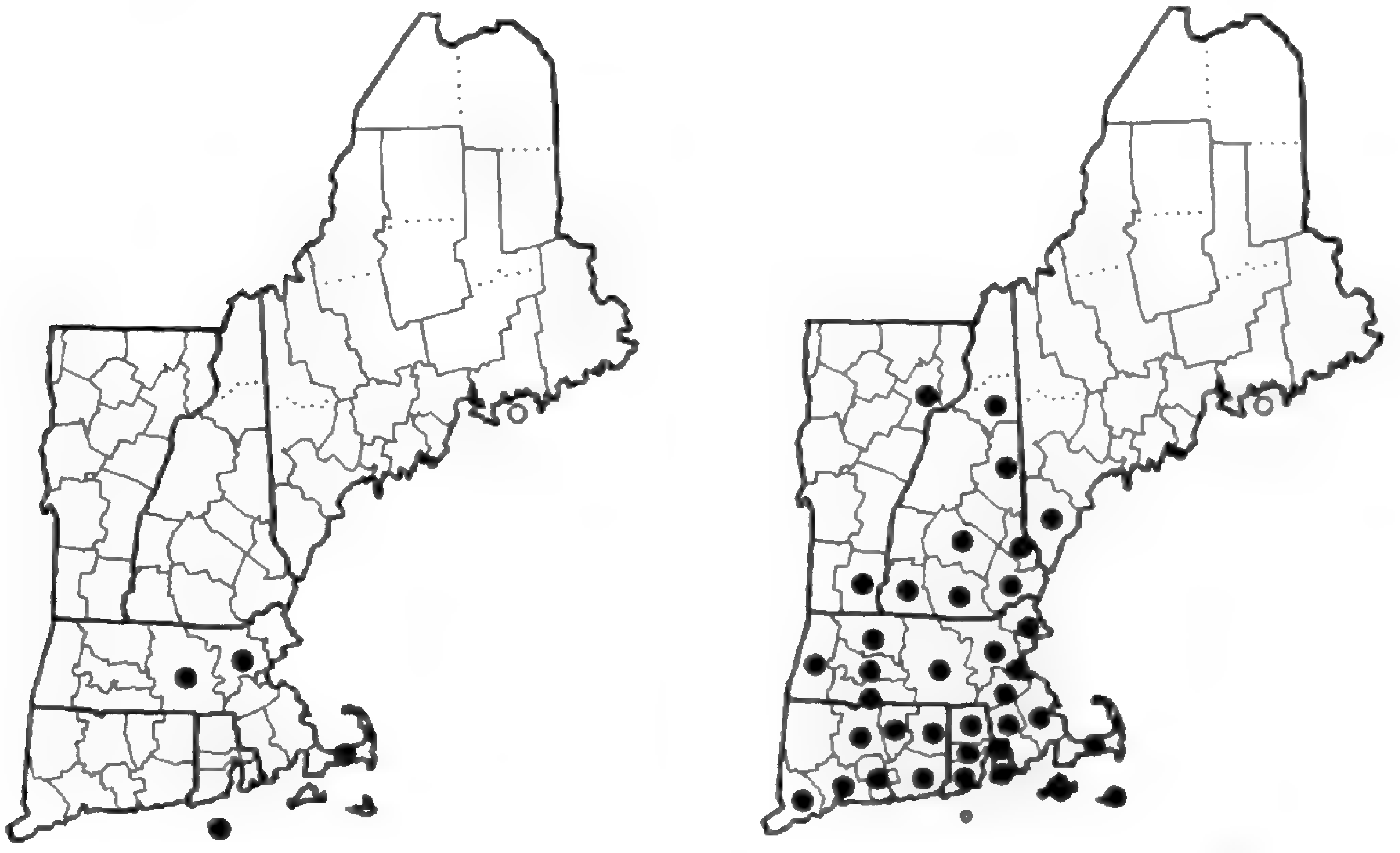


Panicum linearifolium *Panicum meridionale*



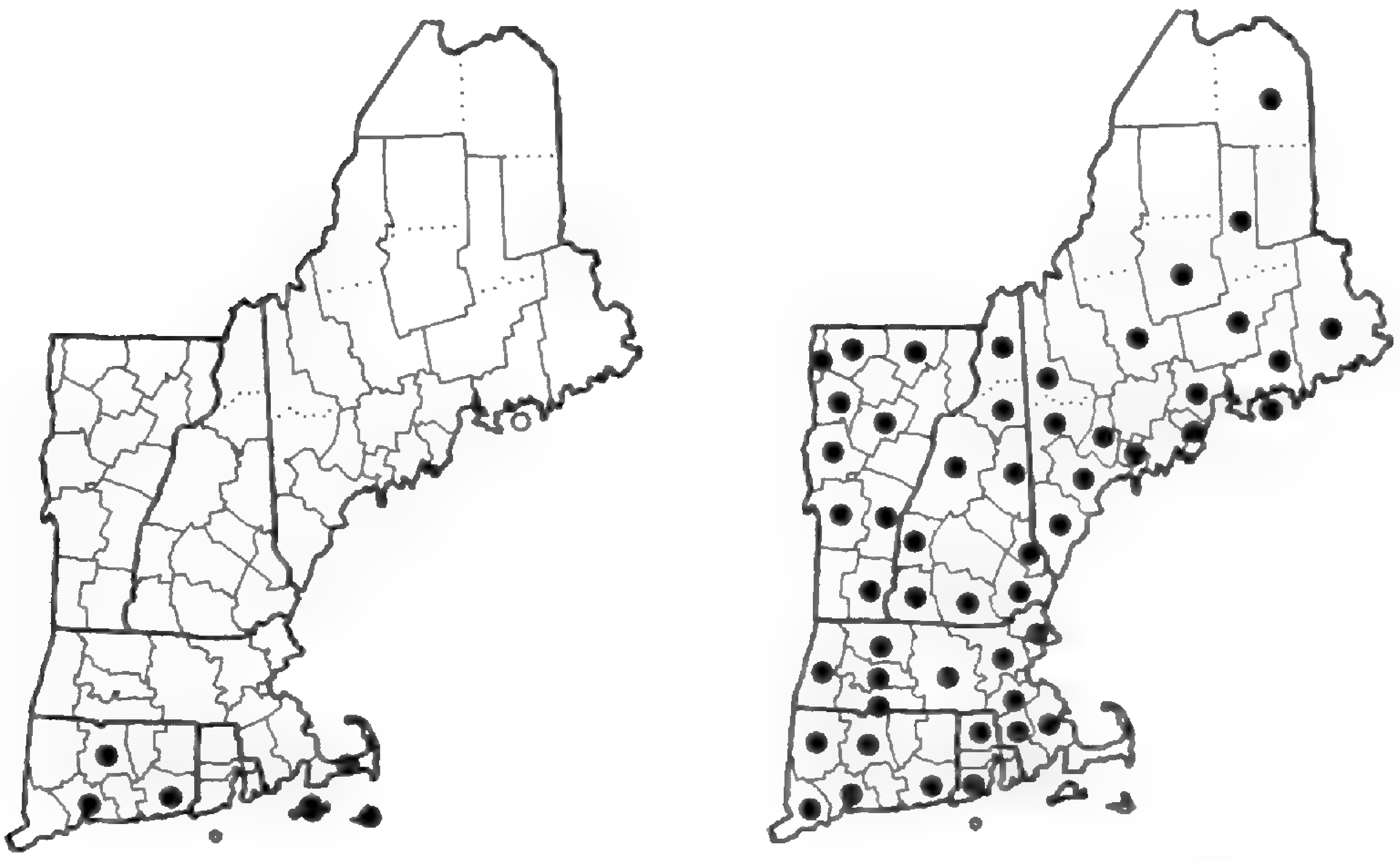
Panicum microcarpon *PANICUM MILIACEUM*

Figure 59. Distribution maps for *Panicum linearifolium, P. meridionale, P. microcarpon* and *P. MILIACEUM.*



Panicum oligosanthes var. *oligosanthes*

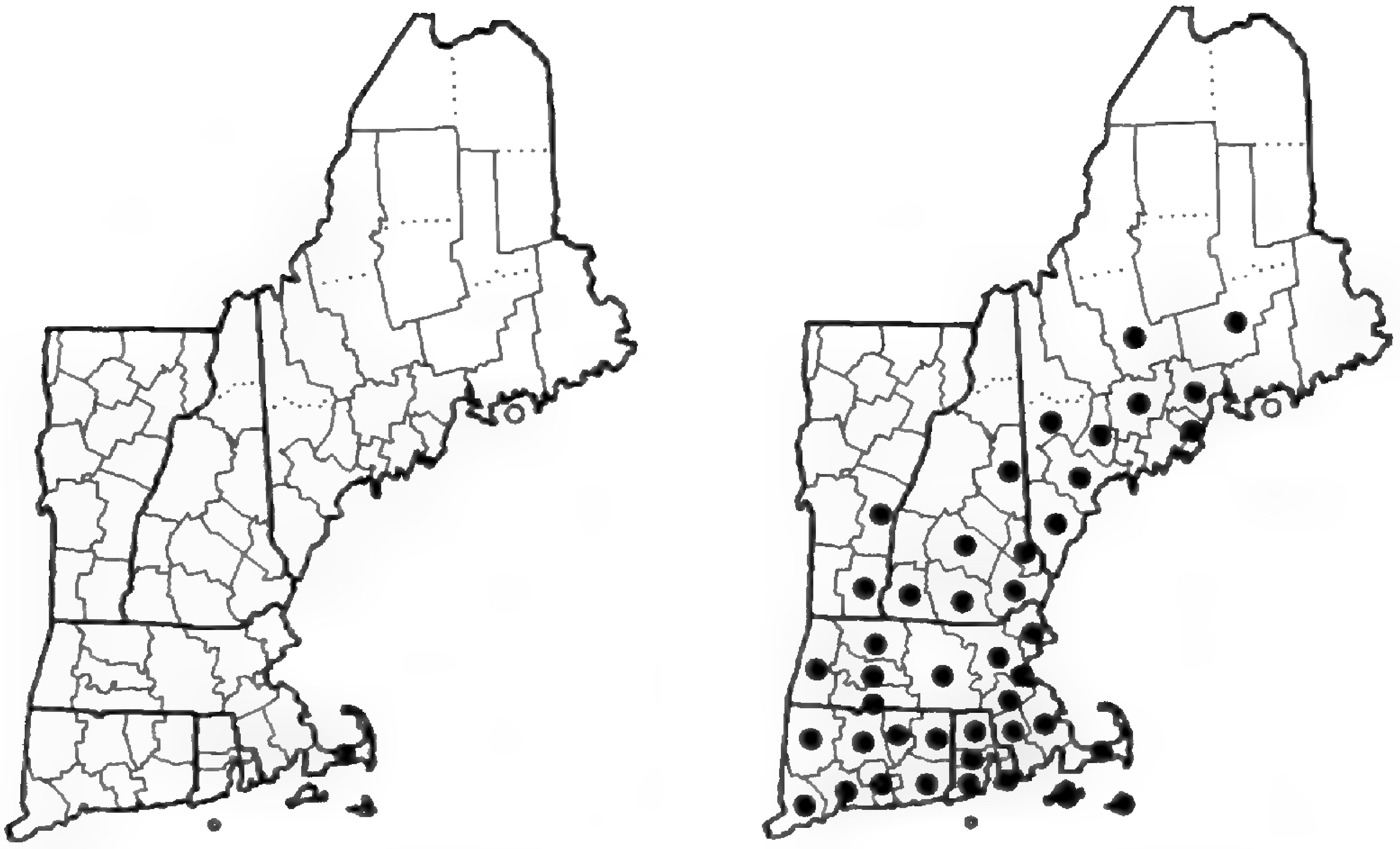
Panicum oligosanthes var. *scribnerianum*



Panicum ovale var. *pseudopubescens*

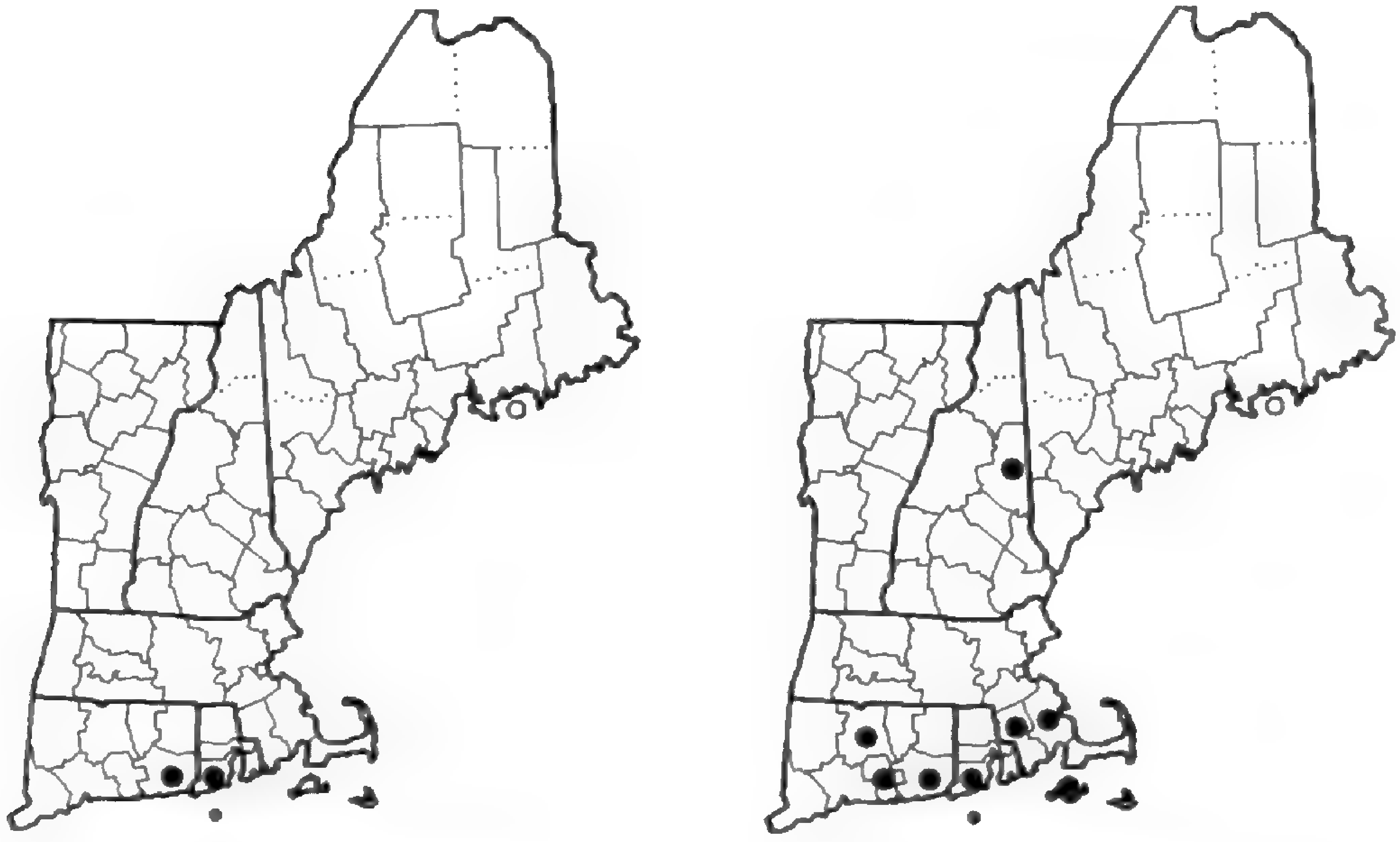
Panicum philadelphicum

Figure 60. Distribution maps for *Panicum oligosanthes* var. *oligosanthes*, *P. oligosanthes* var. *scribnerianum*, *P. ovale* var. *pseudopubescens* and *P. philadelphicum*.



Panicum polyanthes

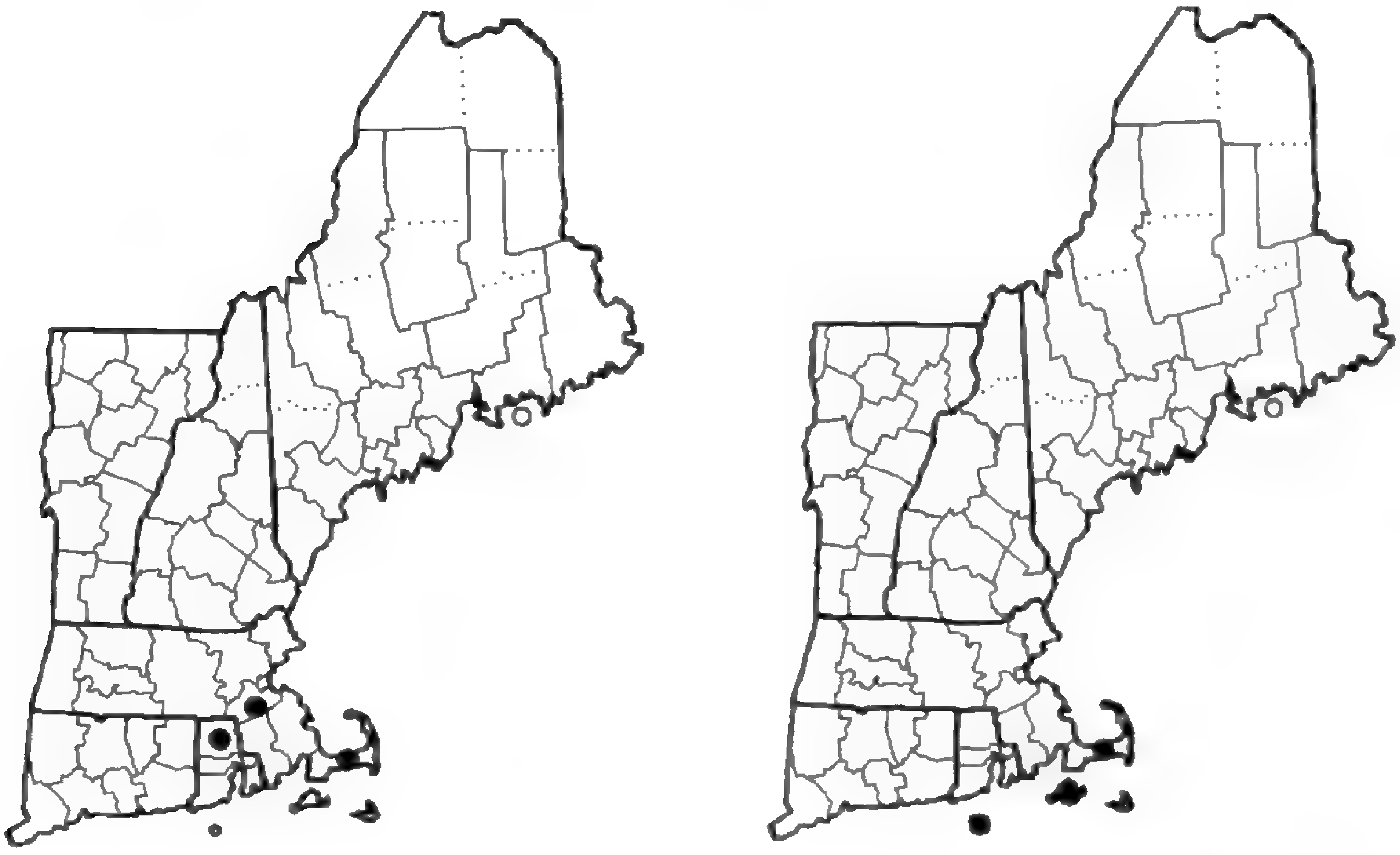
Panicum rigidulum
var. *rigidulum*



Panicum rigidulum
var. *elongatum*

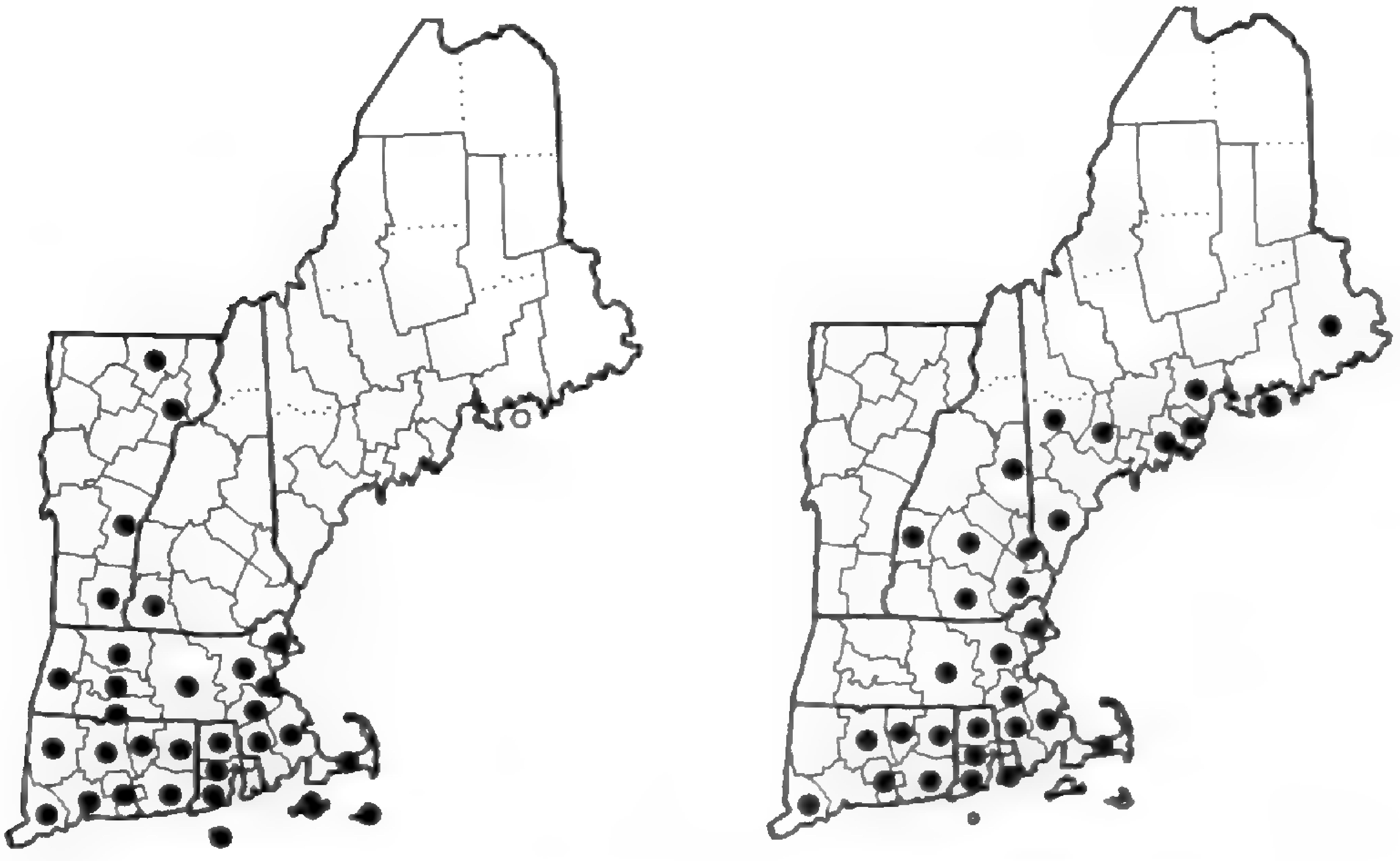
Panicum rigidulum
var. *pubescens*

Figure 61. Distribution maps for *Panicum polyanthes, P. rigidulum* var. *rigidulum, P. rigidulum* var. *elongatum* and *P. rigidulum* var. *pubescens.*



Panicum scabriusculum

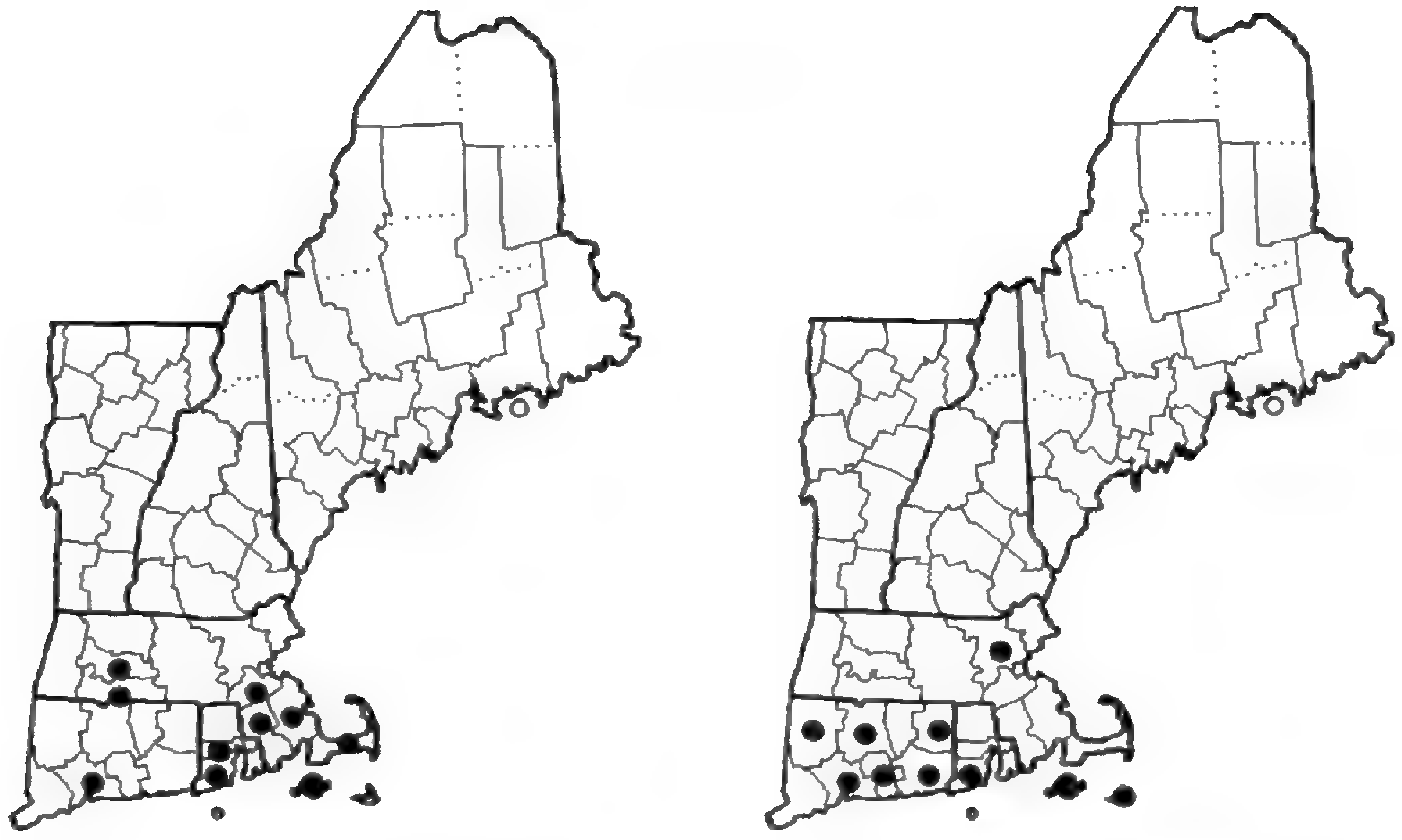
Panicum scoparium



Panicum sphaerocarpon

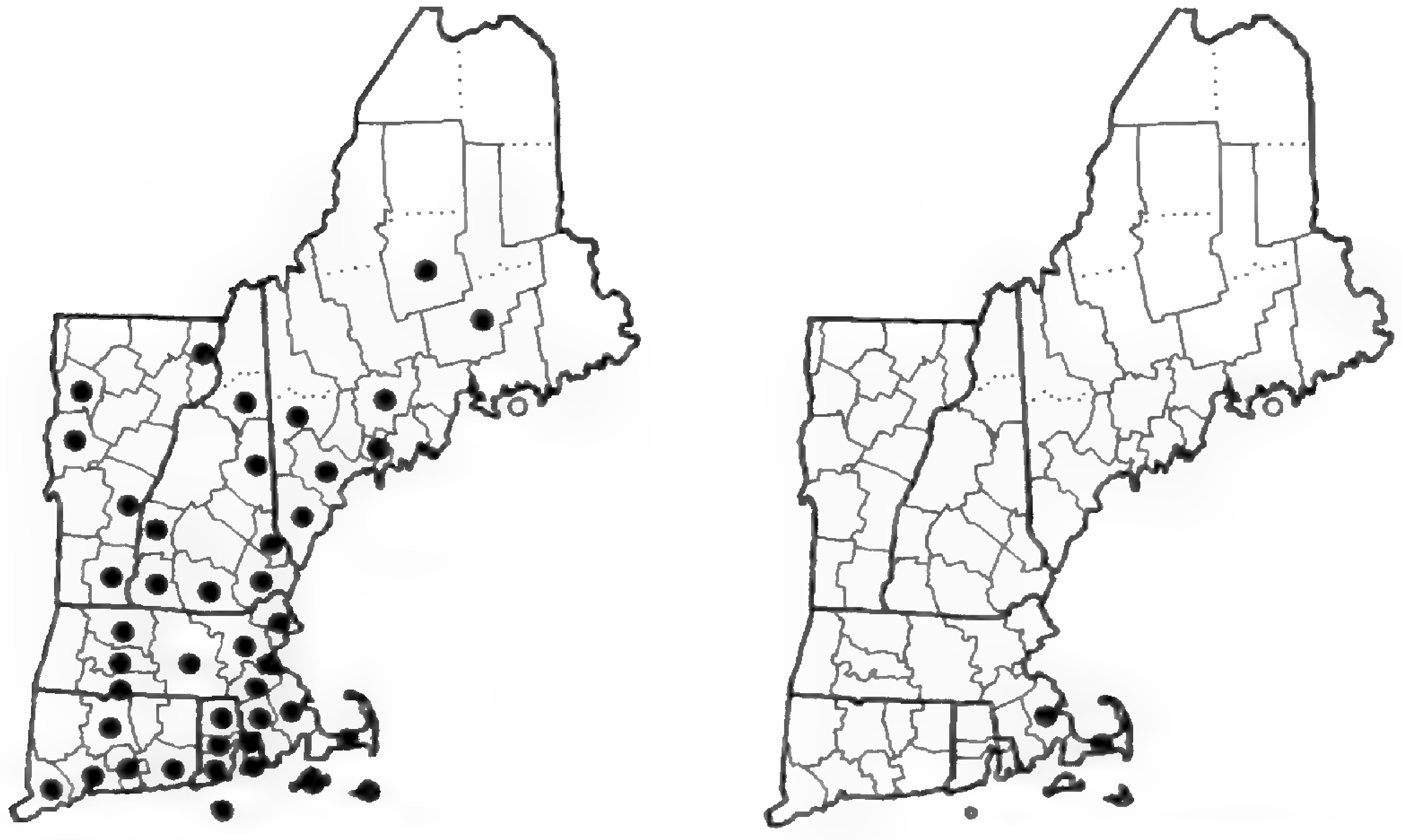
Panicum spretum

Figure 62. Distribution maps for *Panicum scabriusculum, P. scoparium, P. sphaerocarpon* and *P. spretum.*



Panicum verrucosum

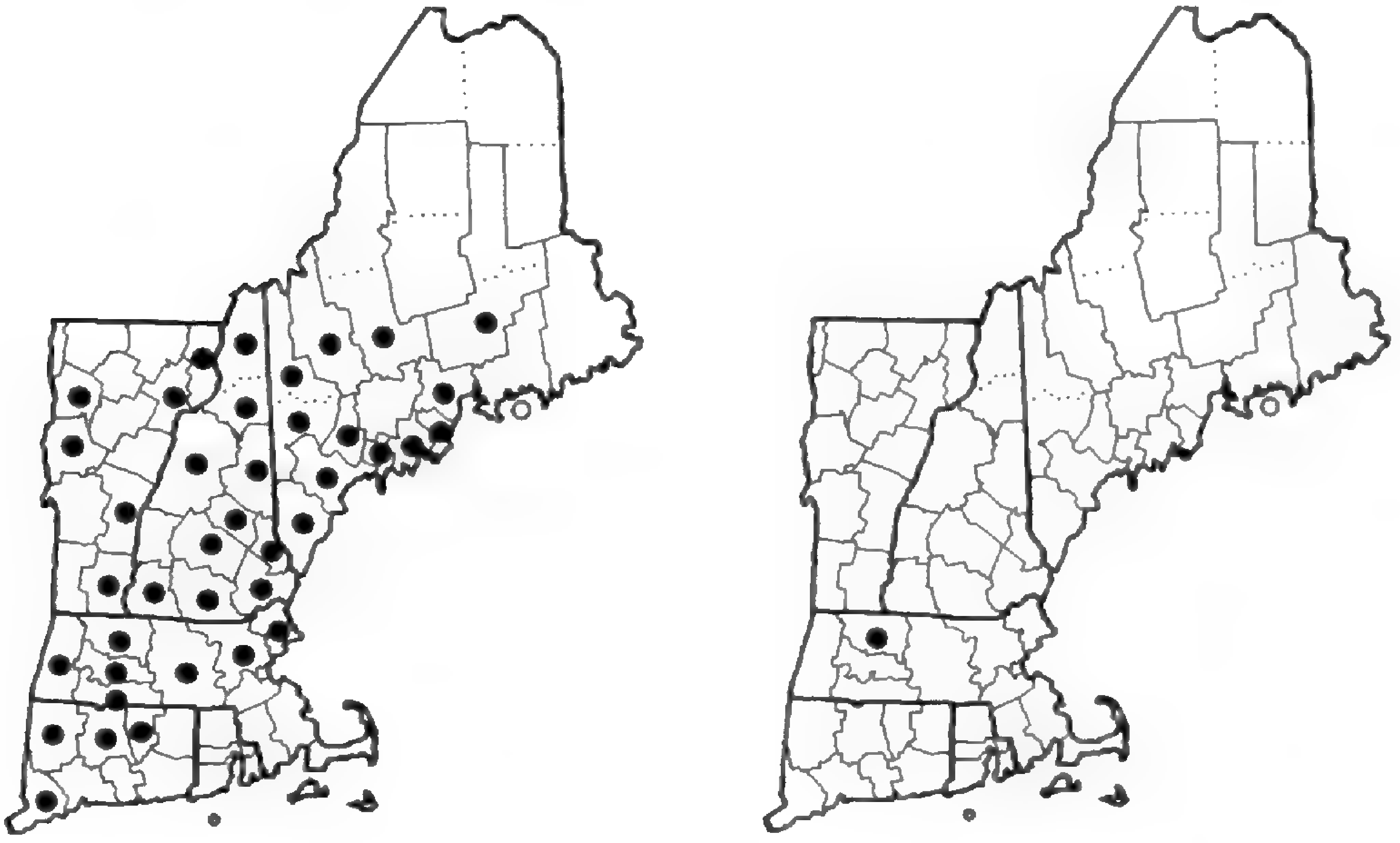
Panicum villosissimum



Panicum virgatum

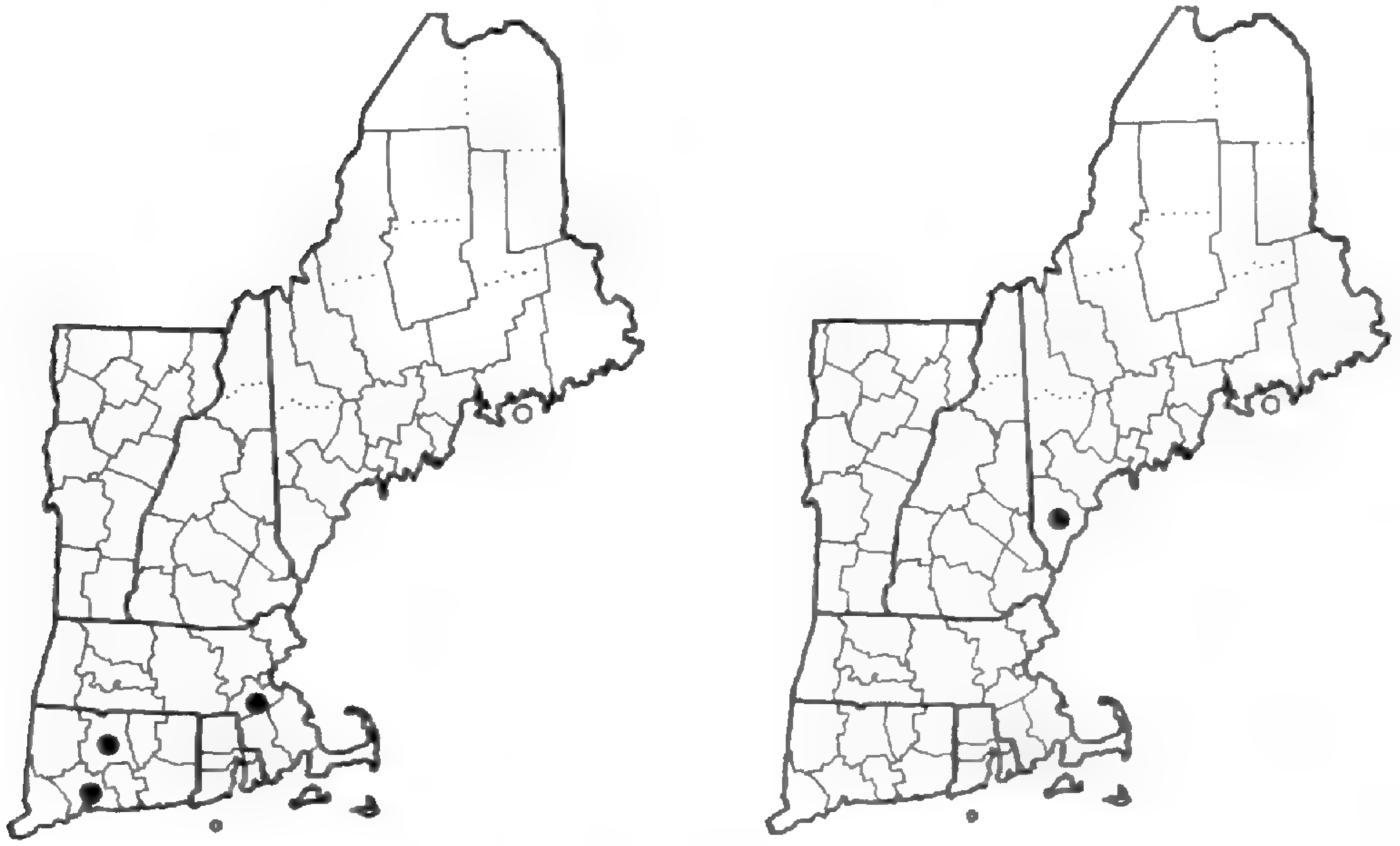
Panicum wrightianum

Figure 63. Distribution maps for *Panicum verrucosum, P. villosissimum, P. virgatum* and *P. wrightianum.*



Panicum xanthophysum

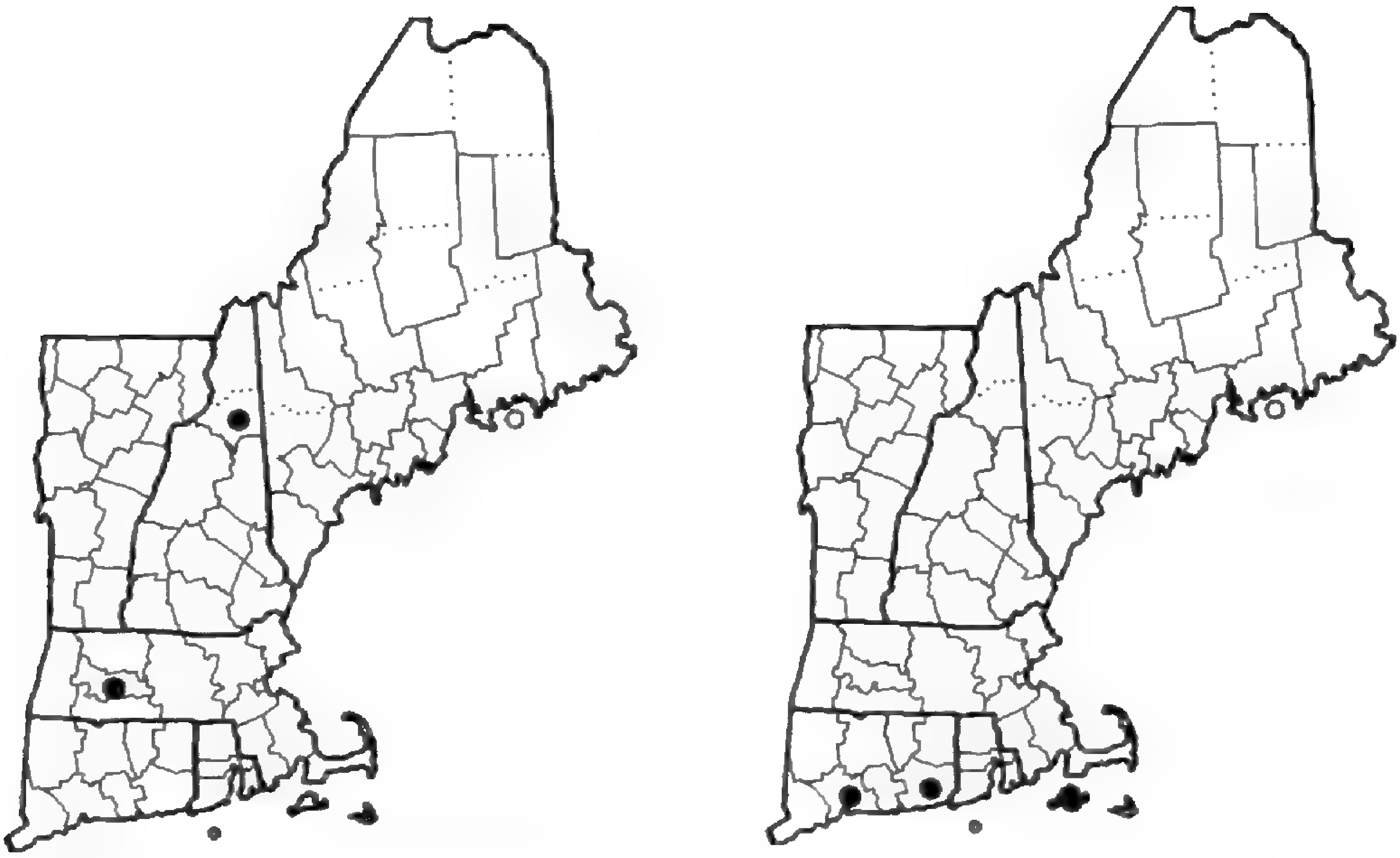
Panicum dichotomum x *P. latifolium*



Panicum x *scoparioides*

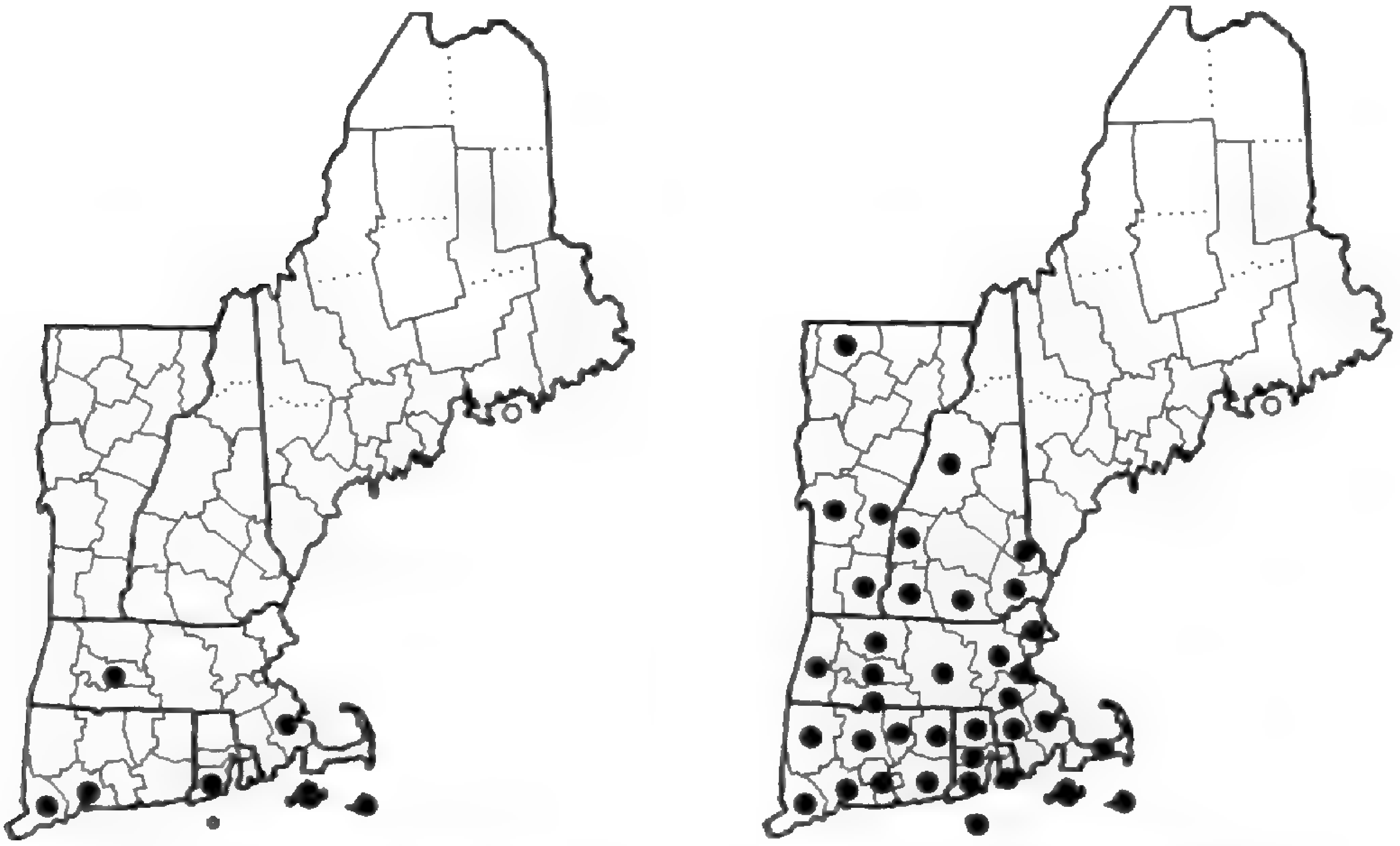
PAPPOPHORUM VAGINATUM

Figure 64. Distribution maps for *Panicum xanthophysum*, *P. dichotomum* × *P. latifolium*, *P.* × *scoparioides* and *PAPPOPHORUM VAGINATUM*.



PASCOPYRUM SMITHII

Paspalum laeve

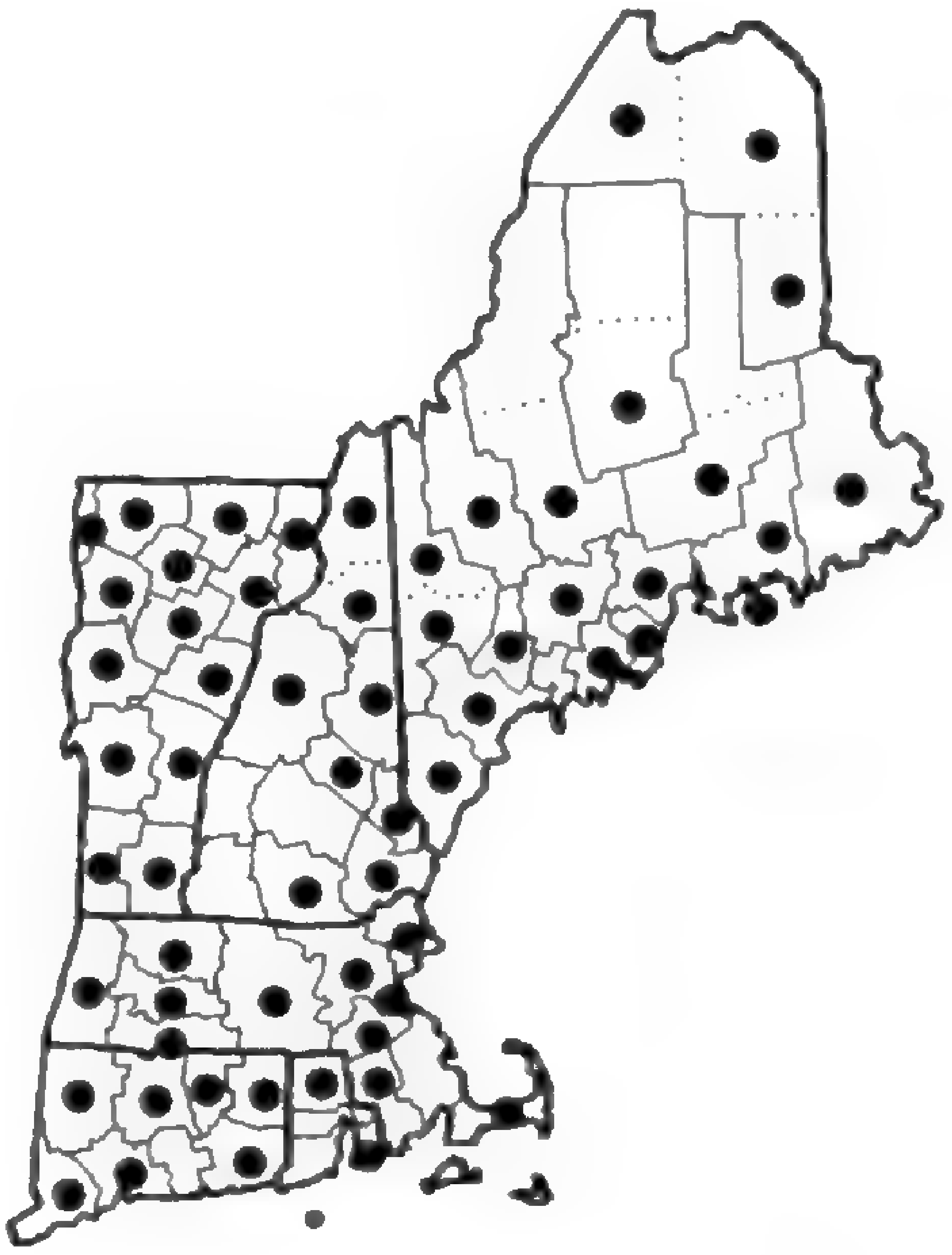


Paspalum setaceum
var. ***setaceum***

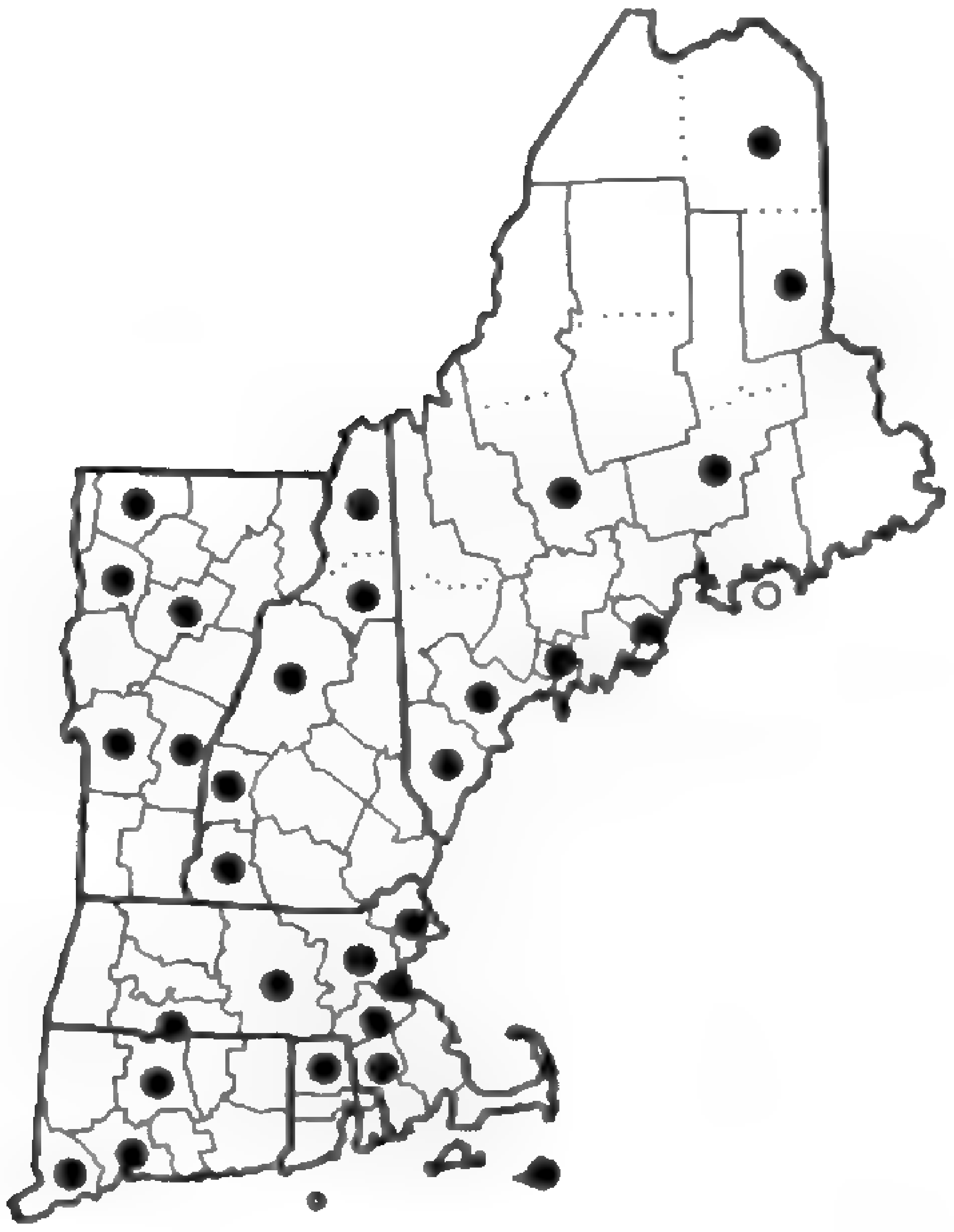
Paspalum setaceum
var. ***muhlenbergii***

Figure 65. Distribution maps for *PASCOPYRUM SMITHII*, *Paspalum laeve*, *P. setaceum* var. *setaceum* and *P. setaceum* var. *muhlenbergii*.

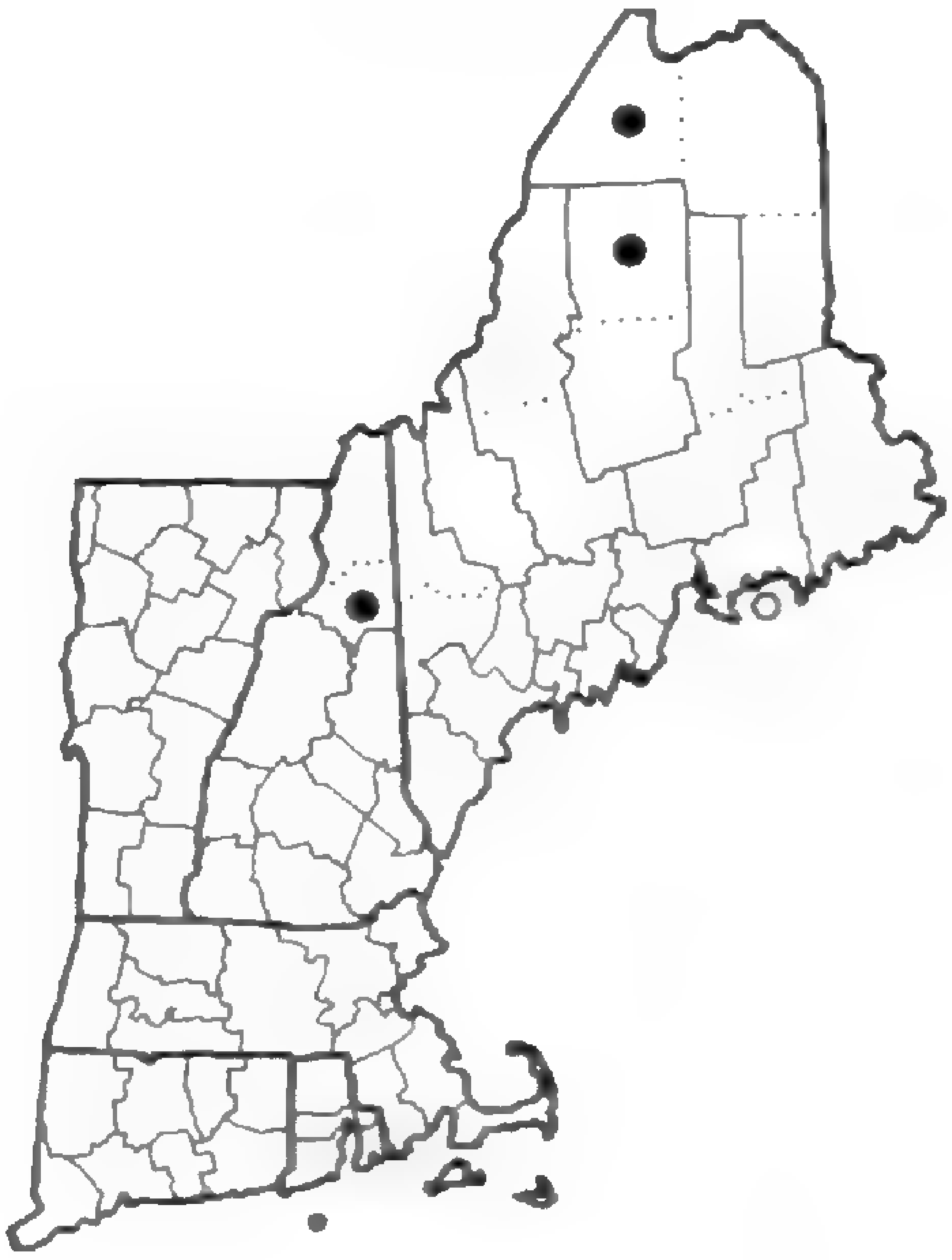
Paspalum setaceum
var. *psammophilum*



Phalaris arundinacea

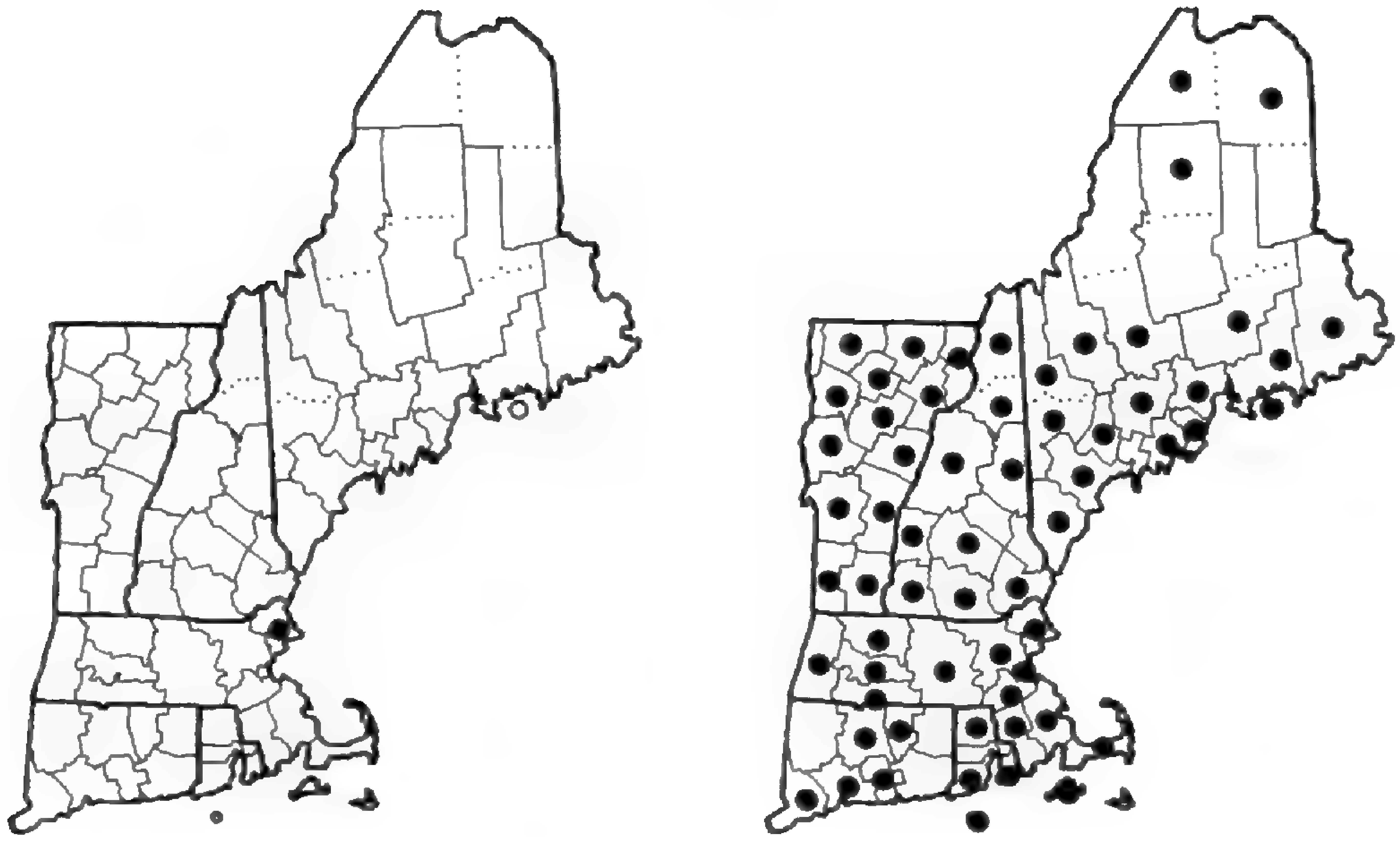


PHALARIS CANARIENSIS



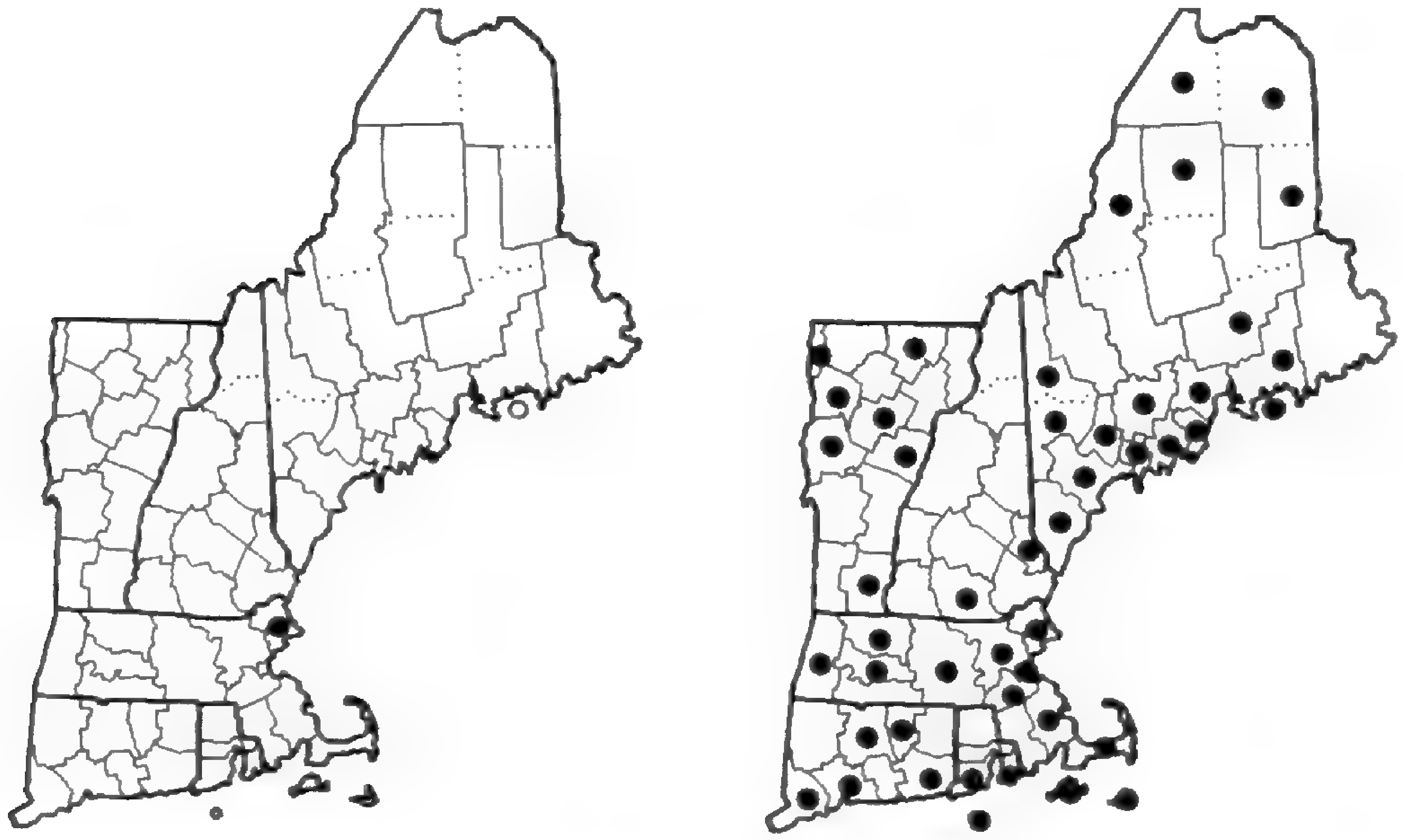
Phleum alpinum

Figure 66. Distribution maps for *Paspalum setaceum* var. *psammophilum*, *Phalaris arundinacea*, *P. CANARIENSIS* and *Phleum alpinum*.



PHLEUM ARENARIUM

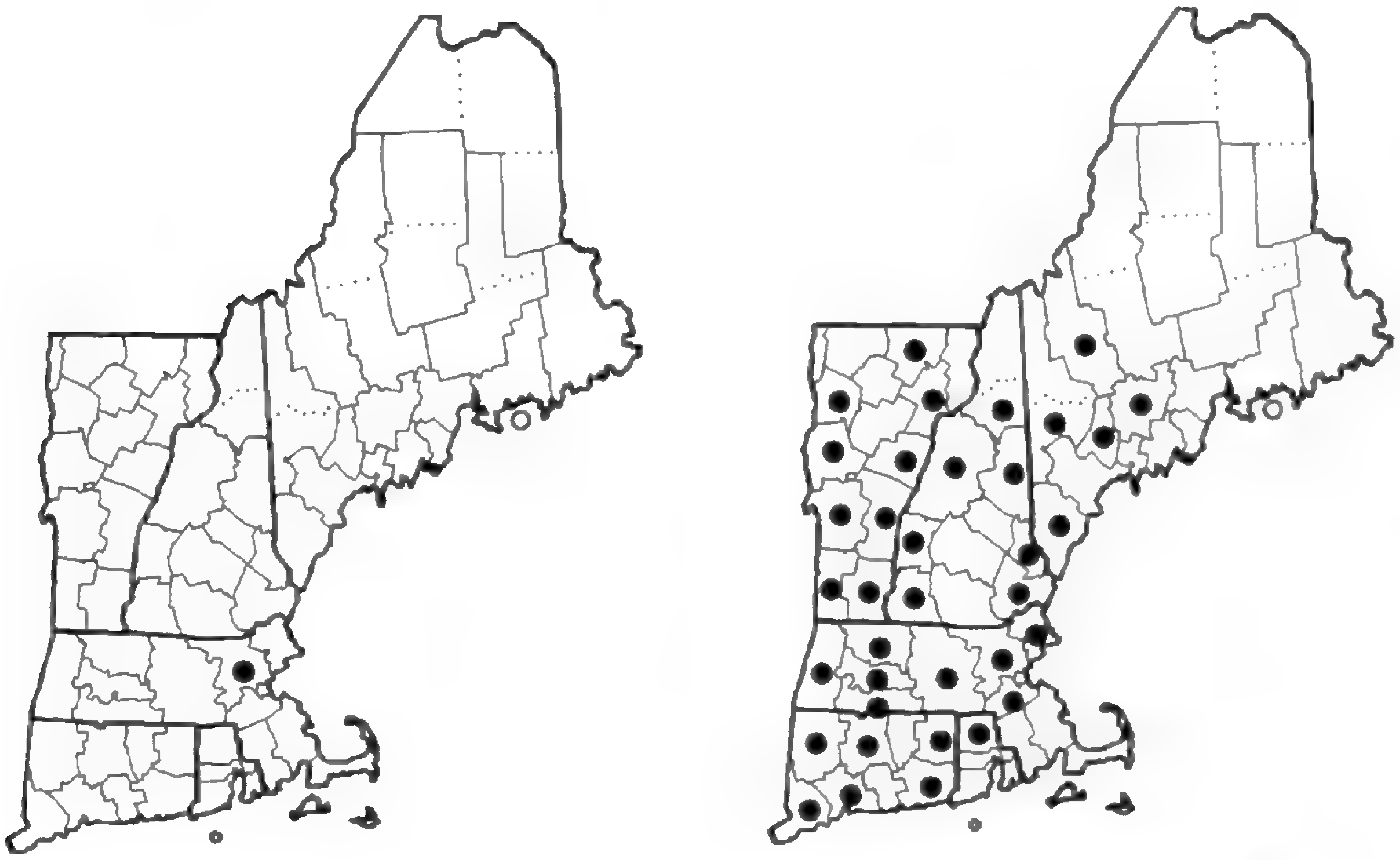
PHLEUM PRATENSE



PHLEUM SUBULATUM

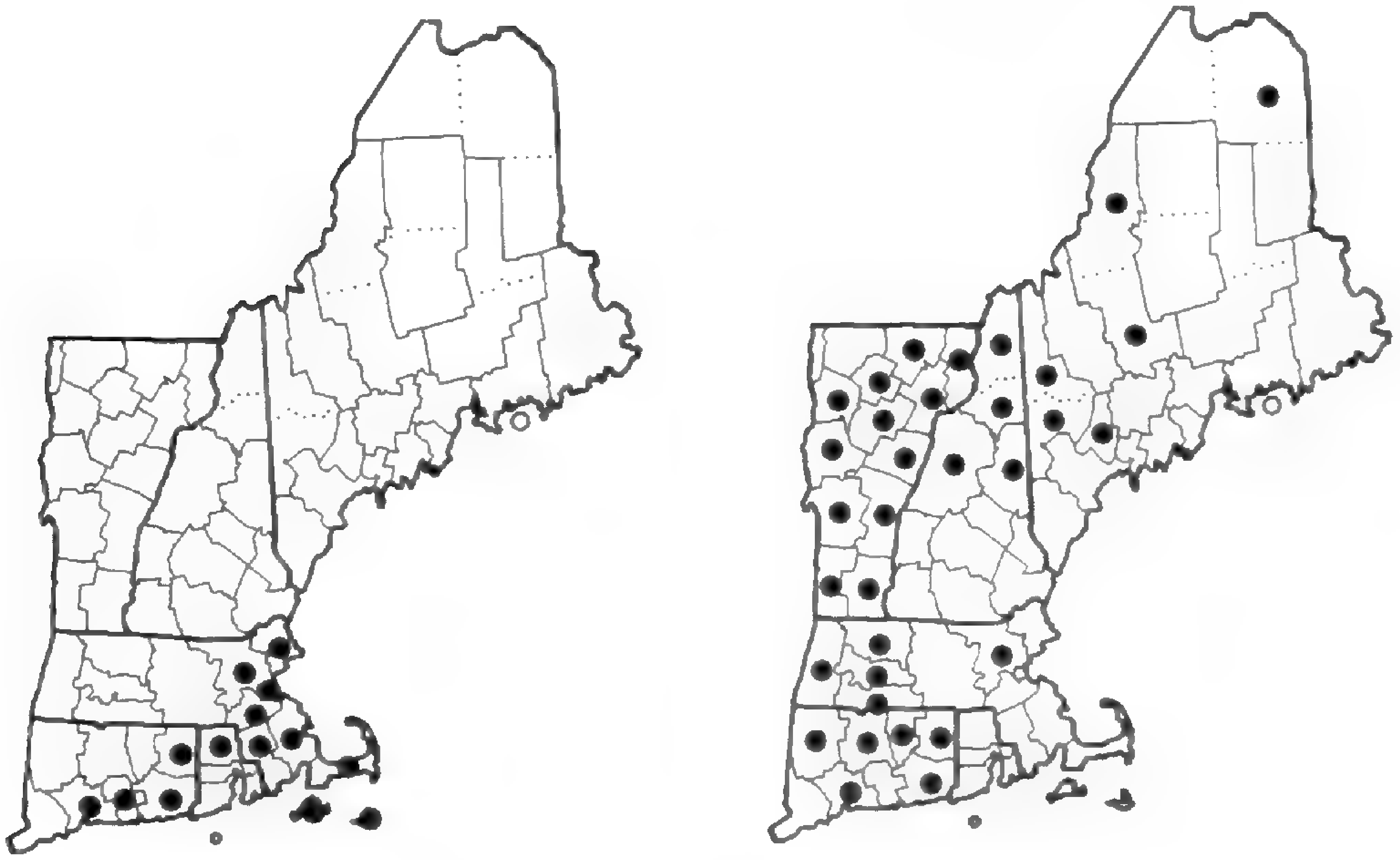
Phragmites australis

Figure 67. Distribution maps for *PHLEUM ARENARIUM, P. PRATENSE, P. SUBULATUM* and *Phragmites australis.*



PHYLLOSTACHYS DULCIS

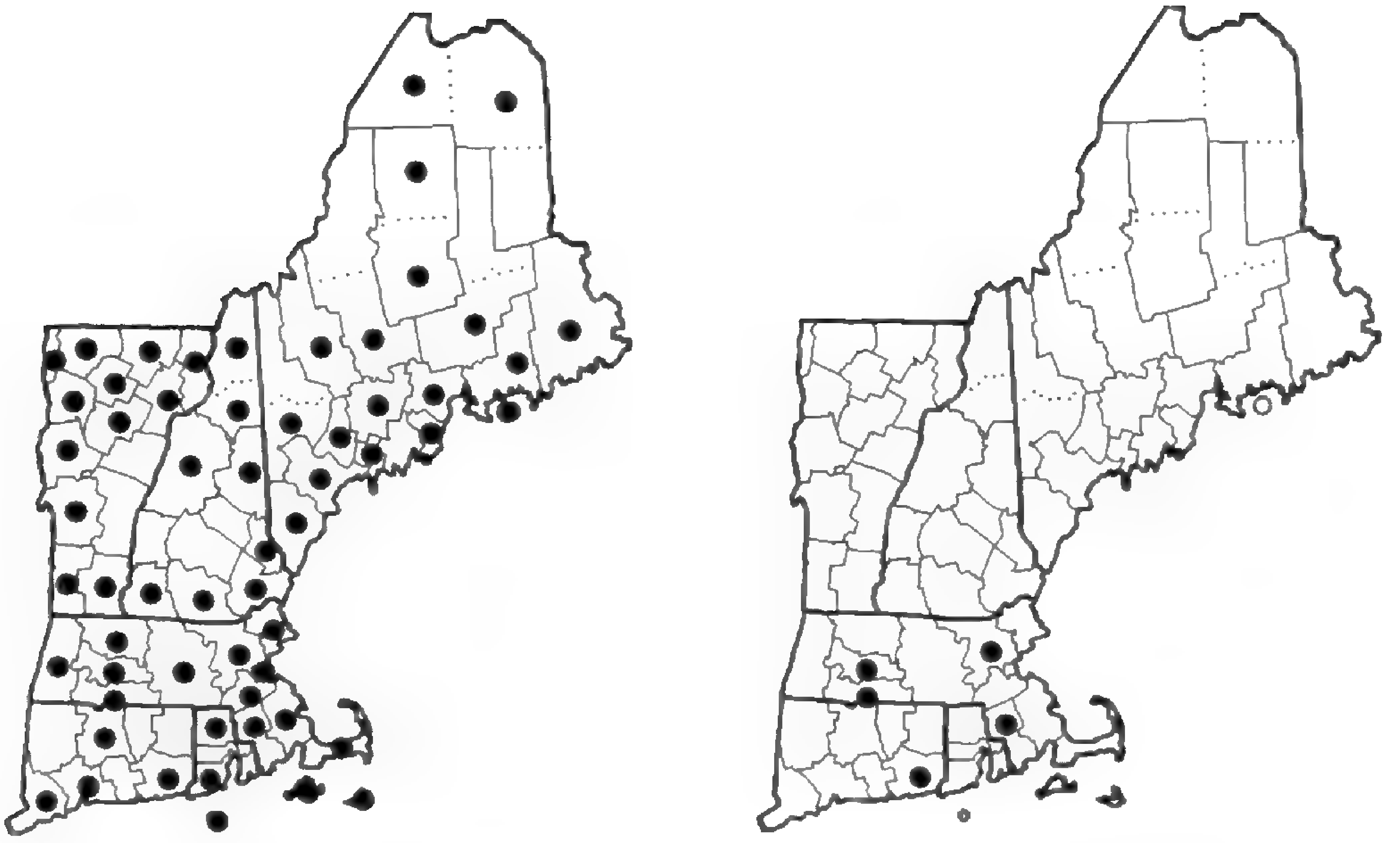
Piptatherum racemosum



Piptochaetium avenaceum

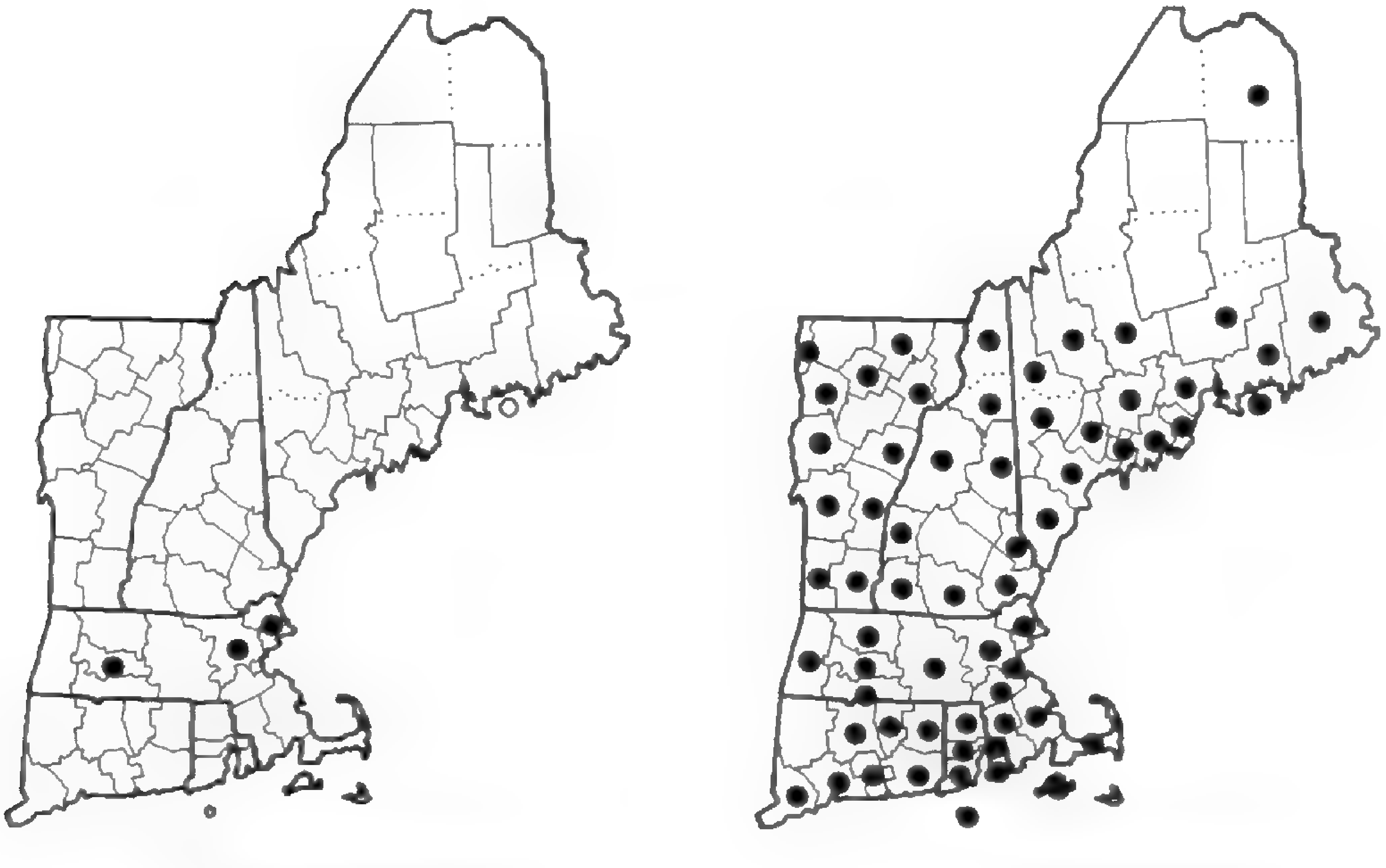
Poa alsodes

Figure 68. Distribution maps for *PHYLLOSTACHYS DULCIS*, *Piptatherum racemosum*, *Piptochaetium avenaceum* and *Poa alsodes*.



POA ANNUA

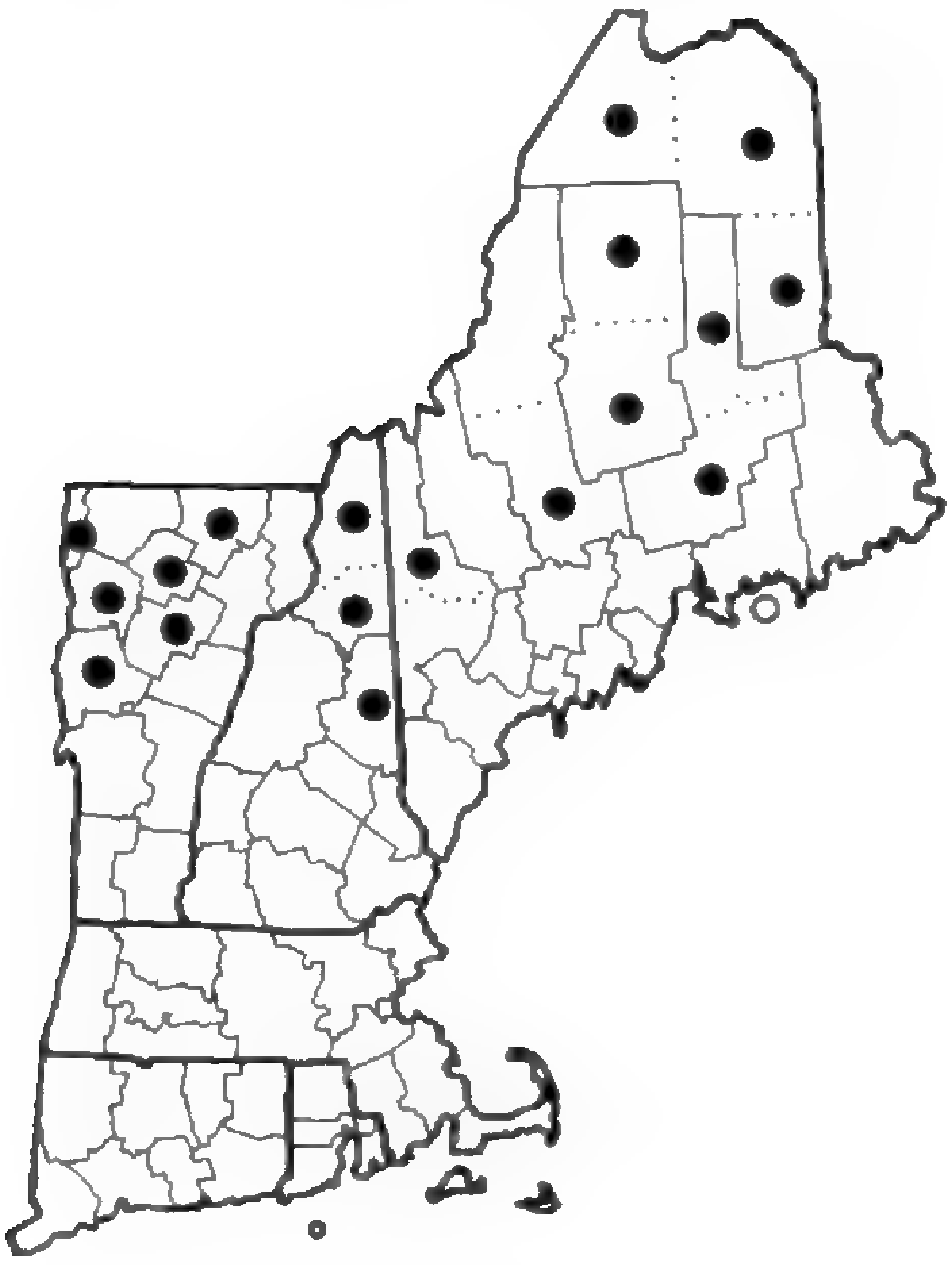
POA BULBOSA



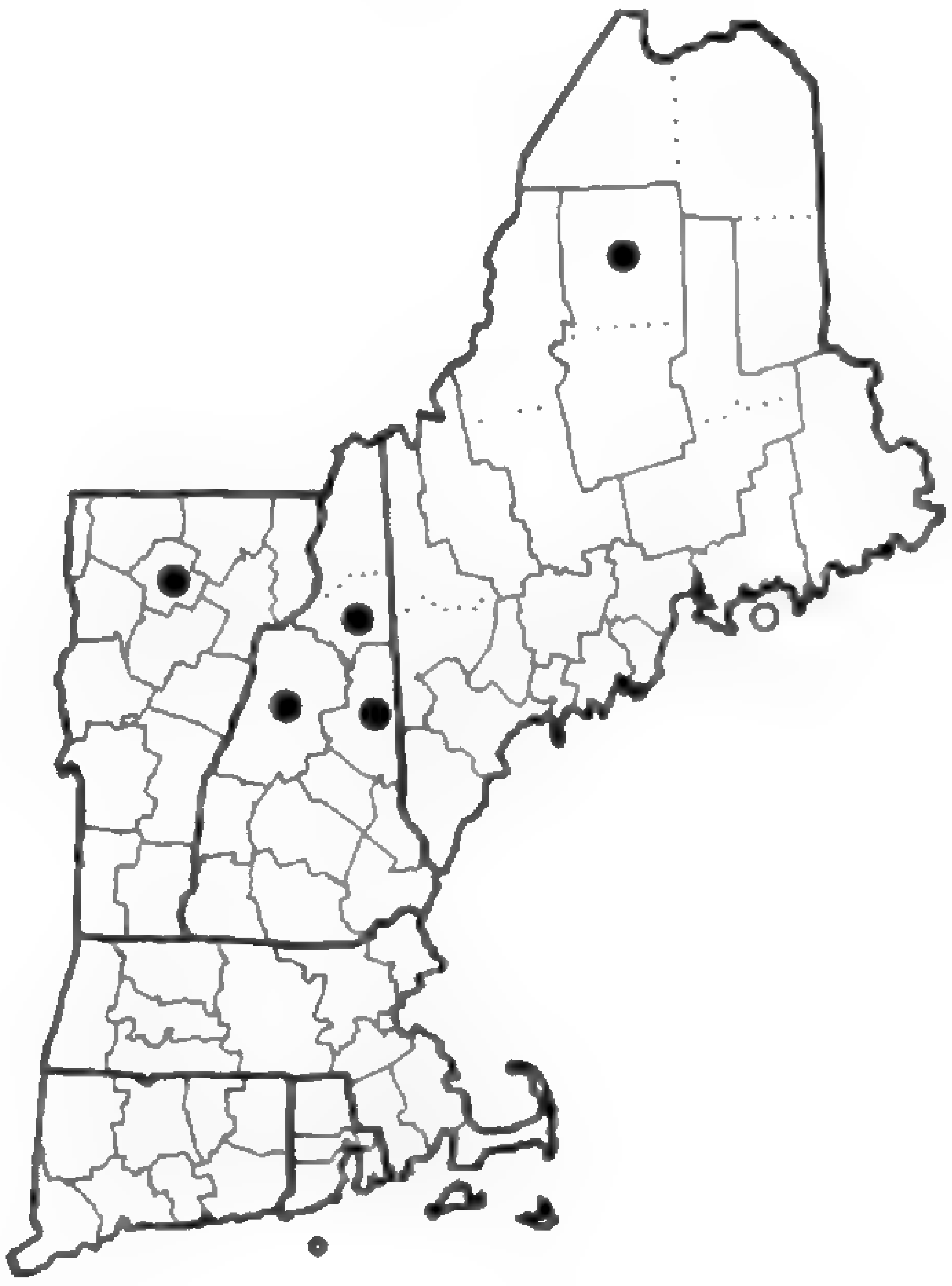
POA CHAPMANIANA

POA COMPRESSA

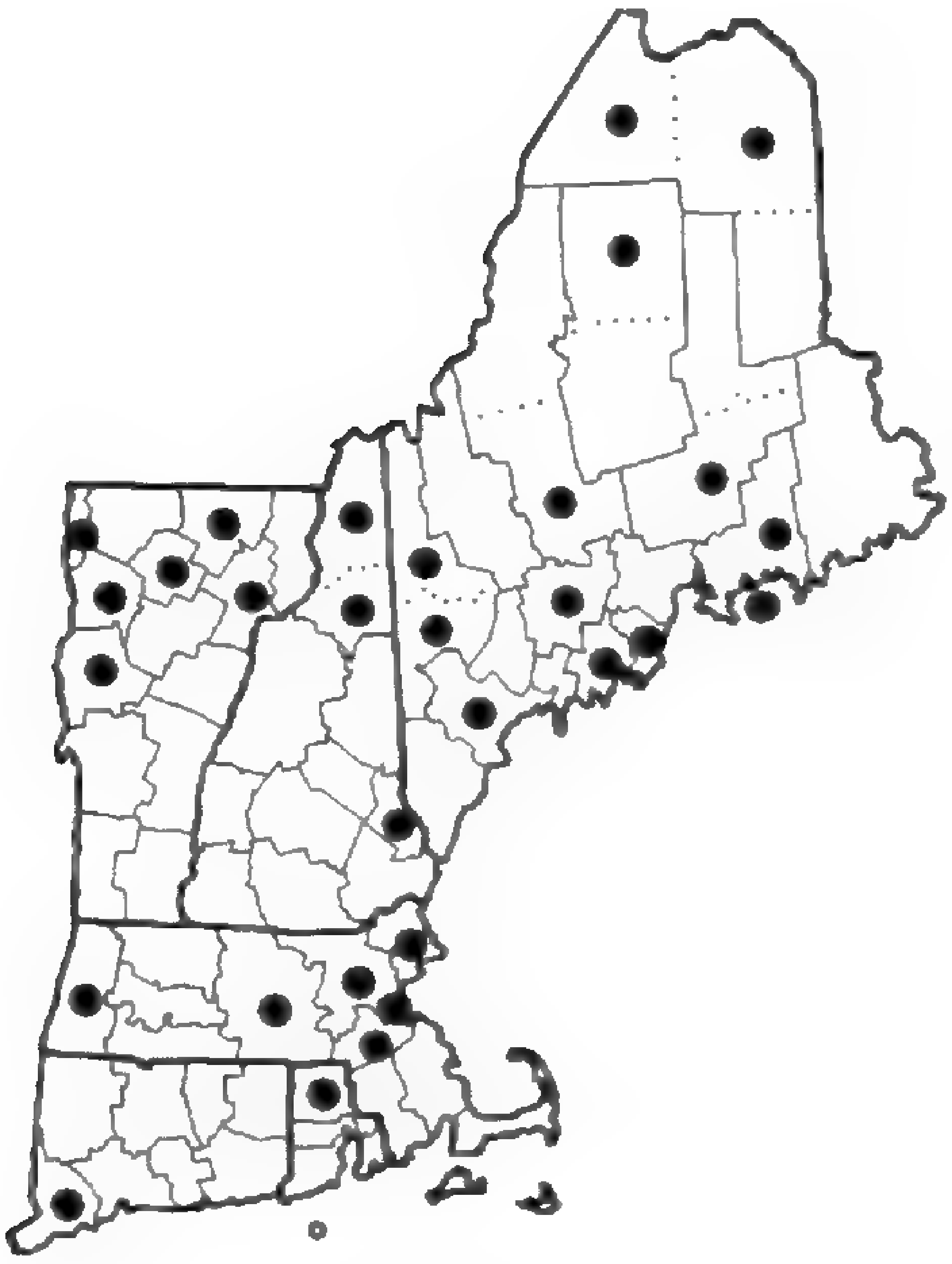
Figure 69. Distribution maps for *POA ANNUA, P. BULBOSA, P. CHAPMANIANA* and *P. COMPRESSA.*



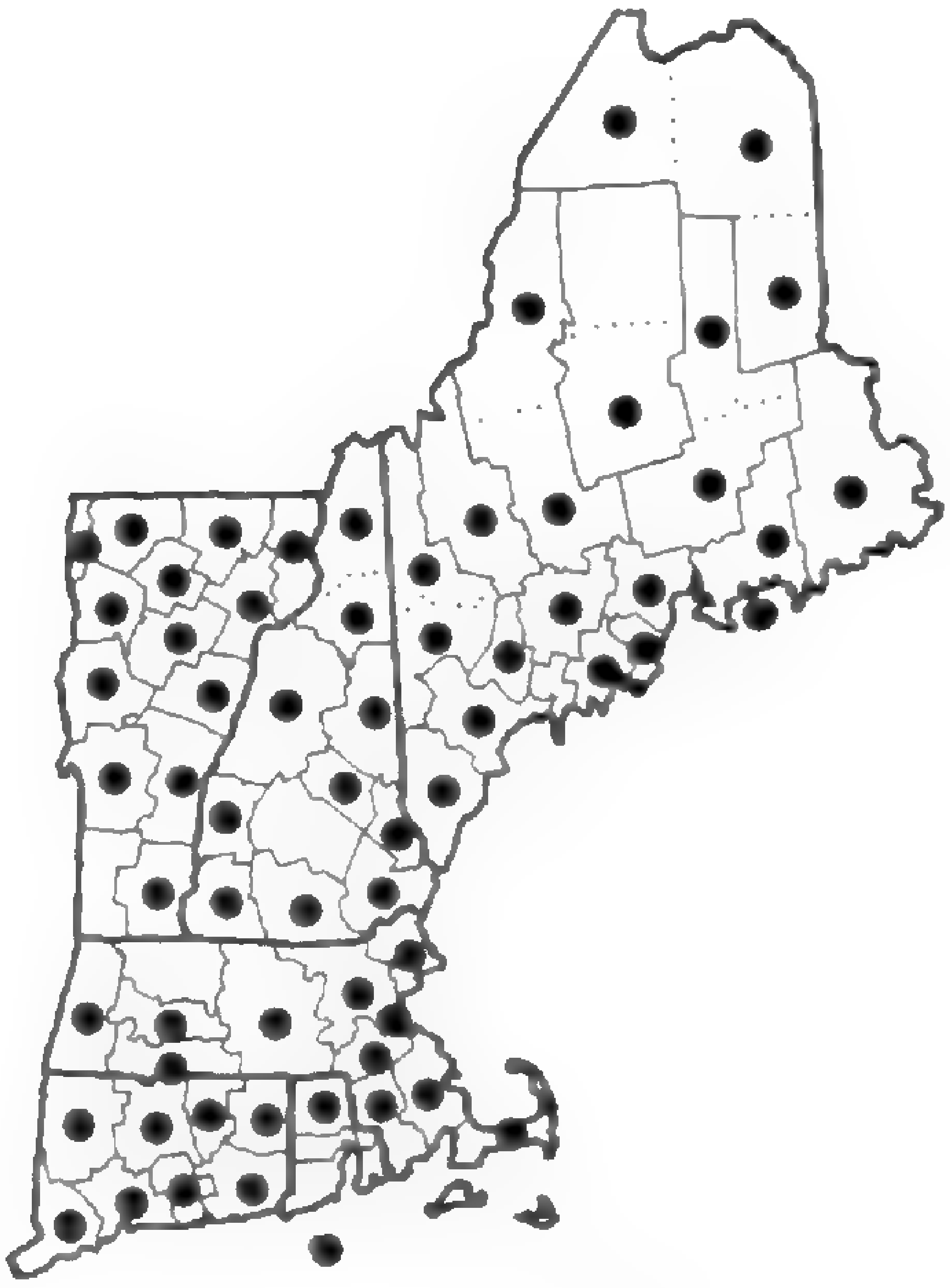
Poa glauca



Poa laxa
subsp. *fernaldiana*

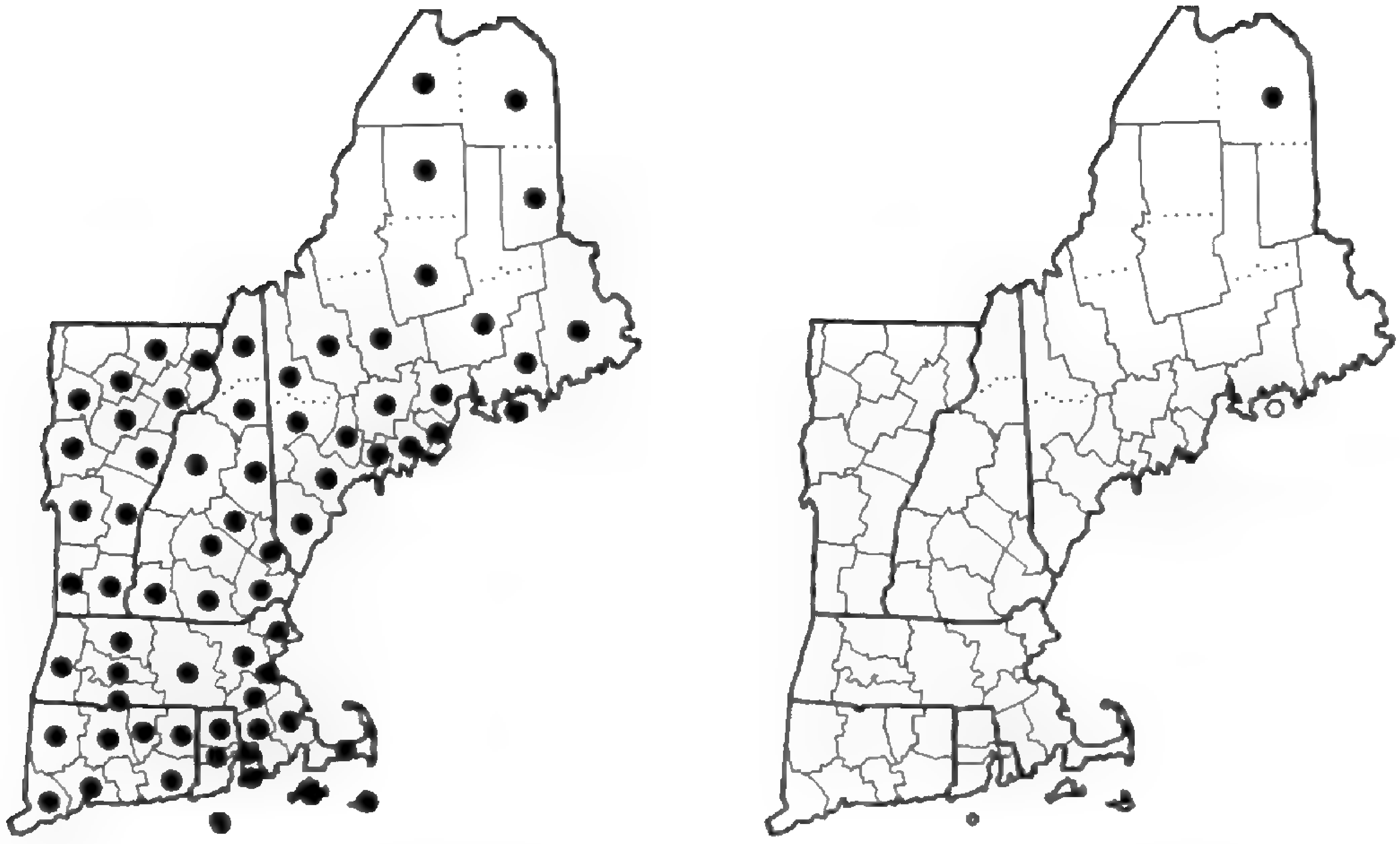


POA NEMORALIS
subsp. *NEMORALIS*



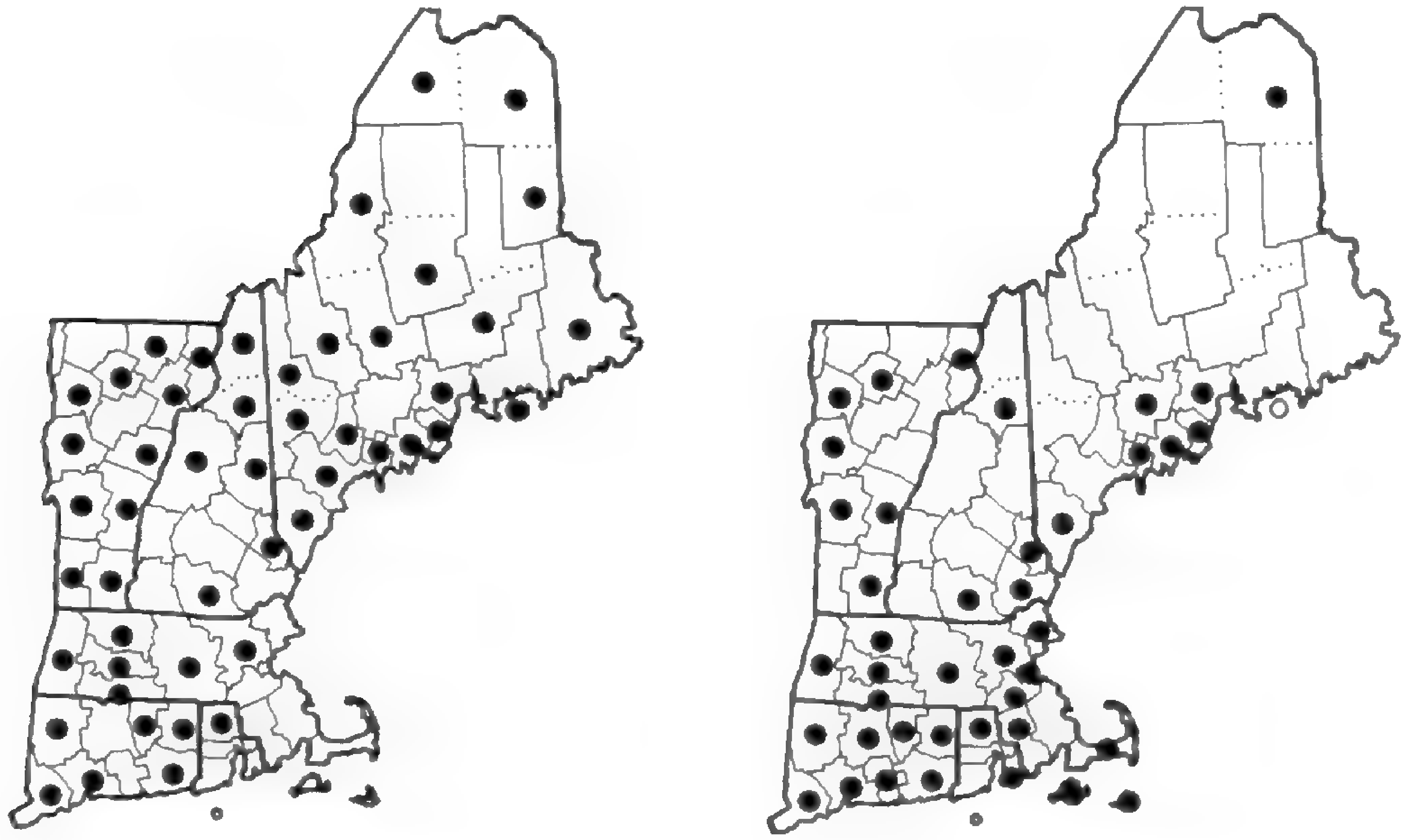
Poa palustris

Figure 70. Distribution maps for *Poa glauca*, *P. laxa* subsp. *fernaldiana*, *P. NEMORALIS* subsp. *NEMORALIS* and *P. palustris*.



POA PRATENSIS
subsp. *PRATENSIS*

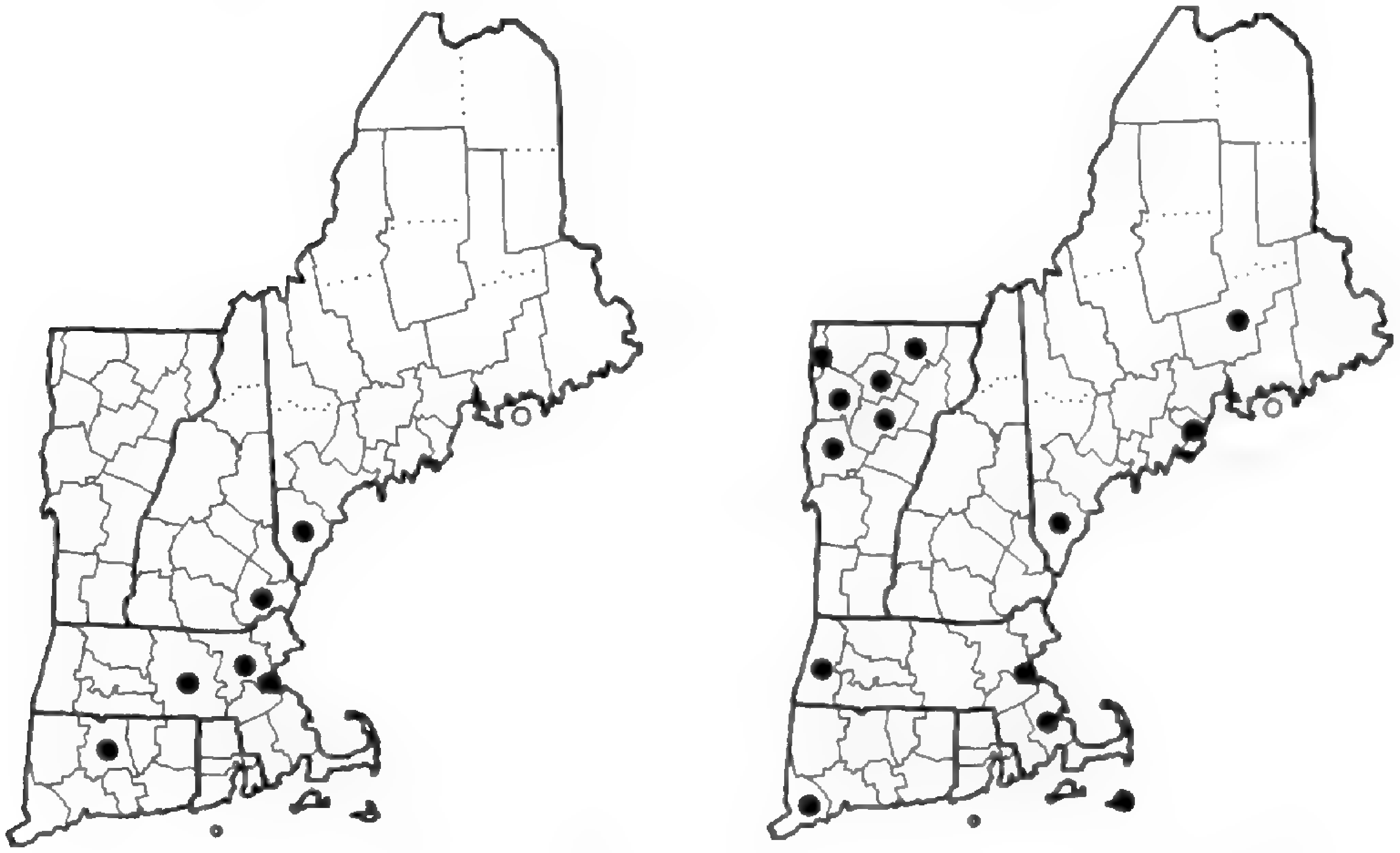
Poa pratensis
subsp. *alpigena*



Poa saltuensis

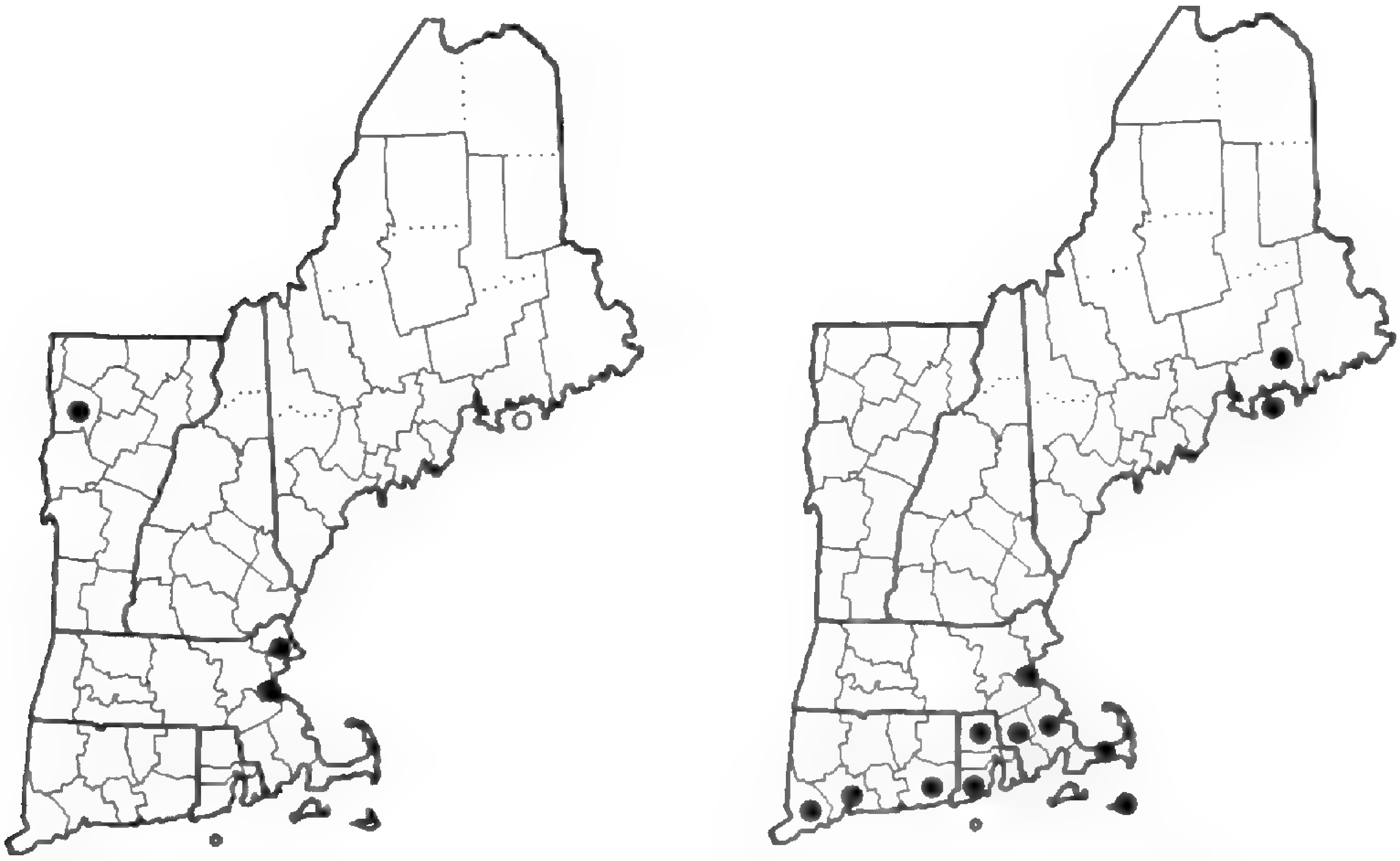
POA TRIVIALIS

Figure 71. Distribution maps for *POA PRATENSIS* subsp. *PRATENSIS*, *P. pratensis* subsp. *alpigena*, *P. saltuensis* and *P. TRIVIALIS*.



POLYPOGON MONSPELIENSIS

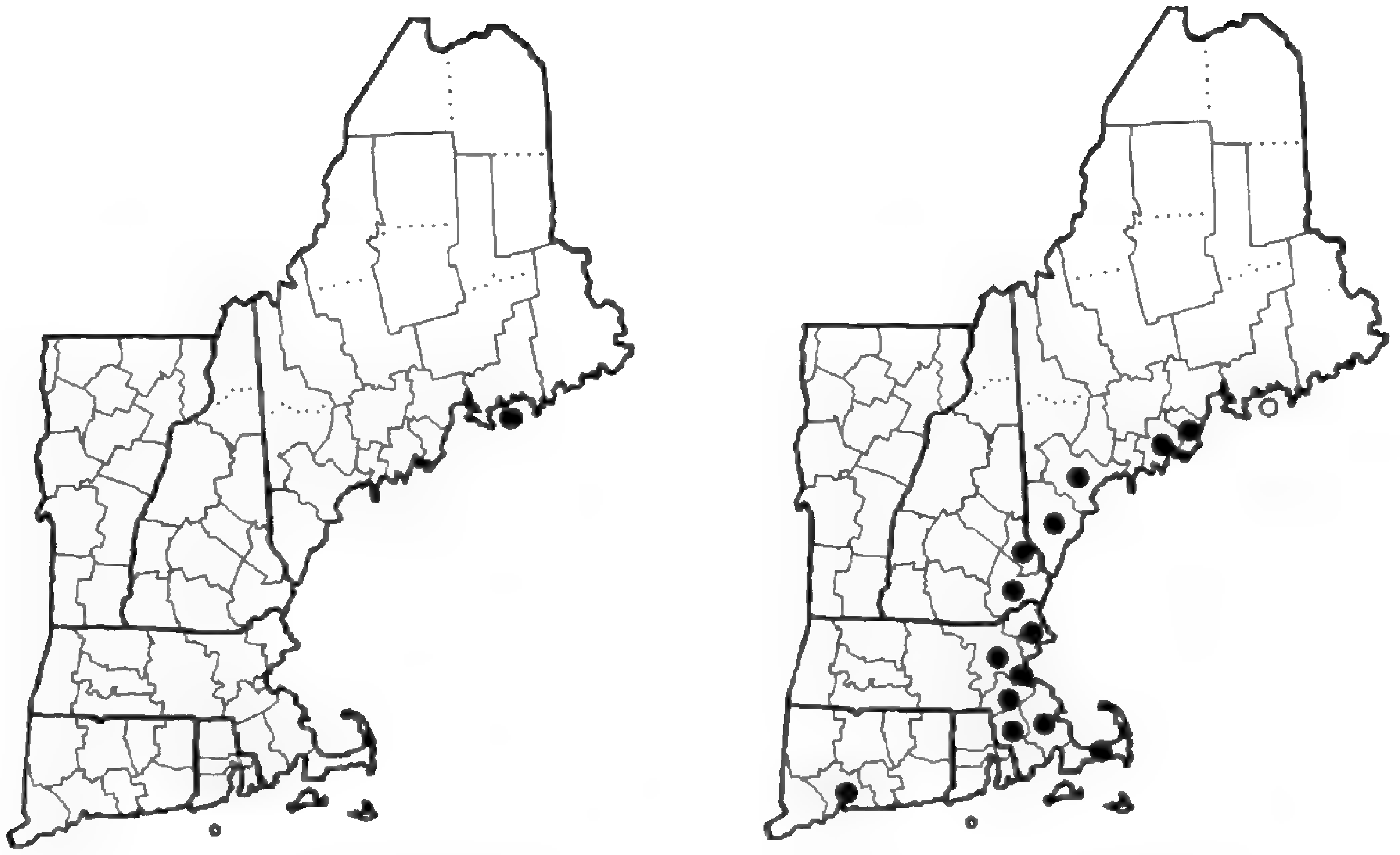
PUCCINELLIA DISTANS
subsp. *DISTANS*



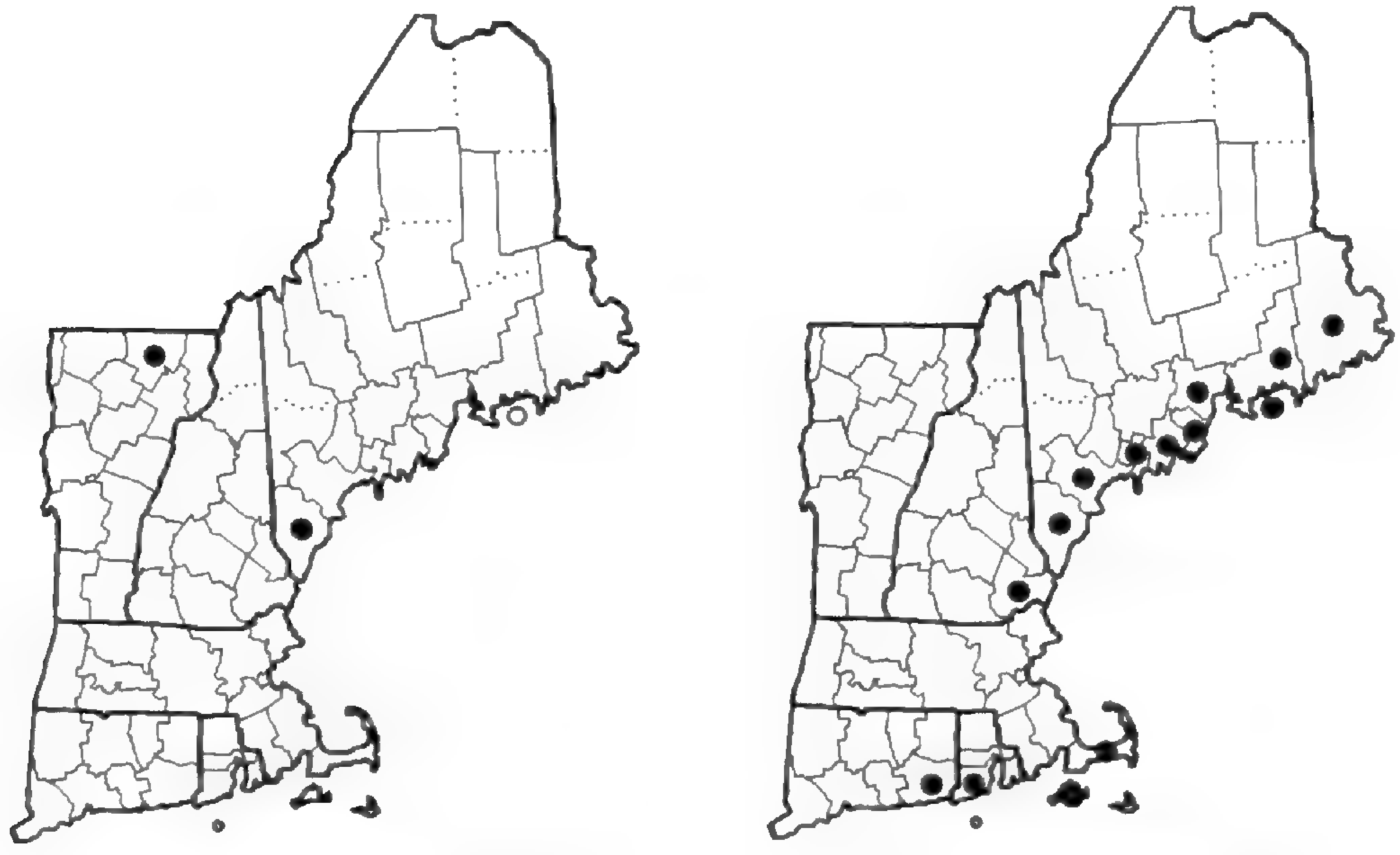
PUCCINELLIA DISTANS
subsp. *BOREALIS*

Puccinellia fasciculata

Figure 72. Distribution maps for *POLYPOGON MONSPELIENSIS, PUCCINELLIA DISTANS* subsp. *DISTANS, P. DISTANS* subsp. *BOREALIS* and *P. fasciculata.*

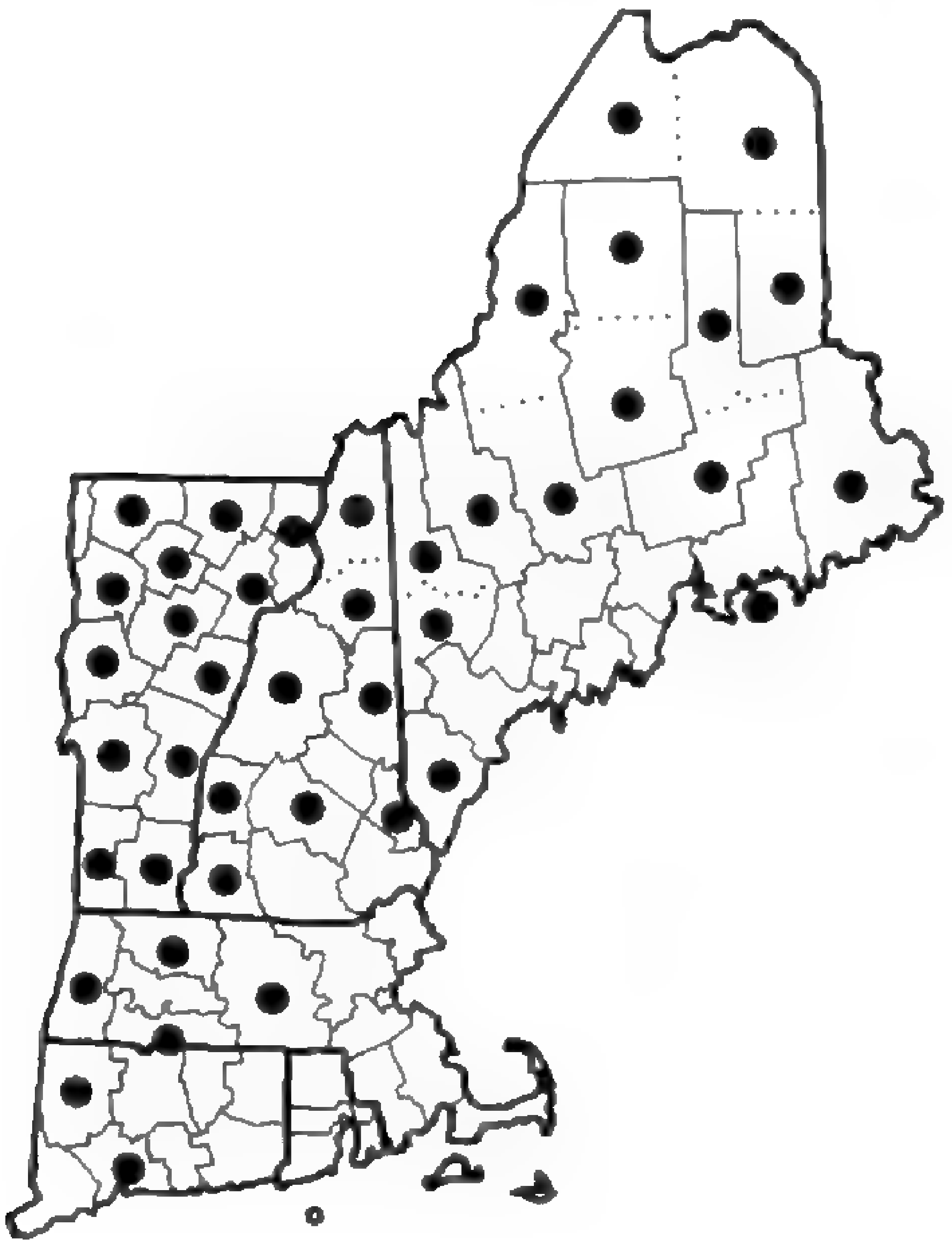


Puccinellia laurentiana *Puccinellia maritima*



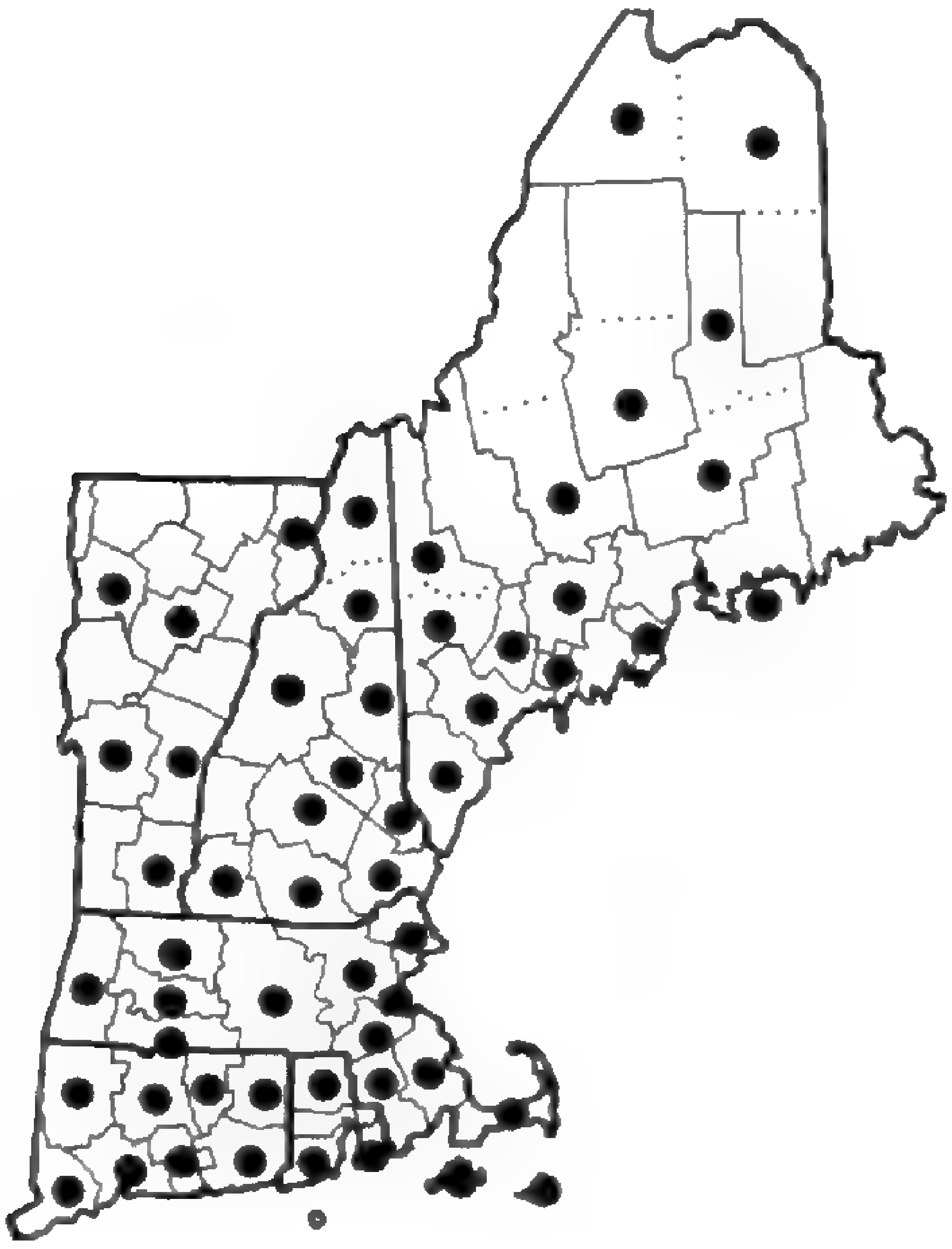
PUCCINELLIA NUTTALLIANA *Puccinellia tenella* subsp. *alaskana*

Figure 73. Distribution maps for *Puccinellia laurentiana*, *P. maritima*, *P. NUTTALLIANA* and *P. tenella* subsp. *alaskana*.

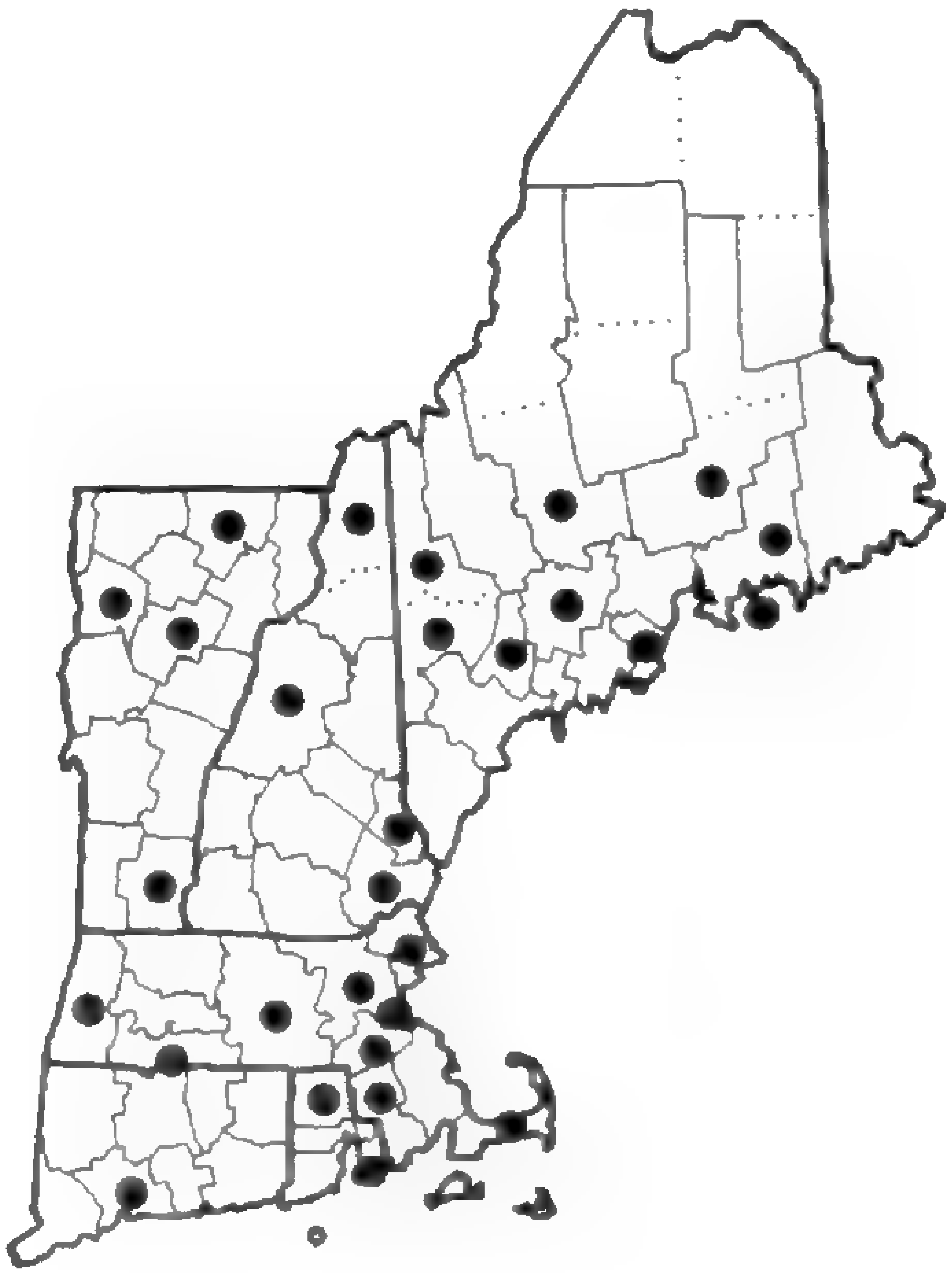


Schizachne purpurascens

Schizachyrium littorale

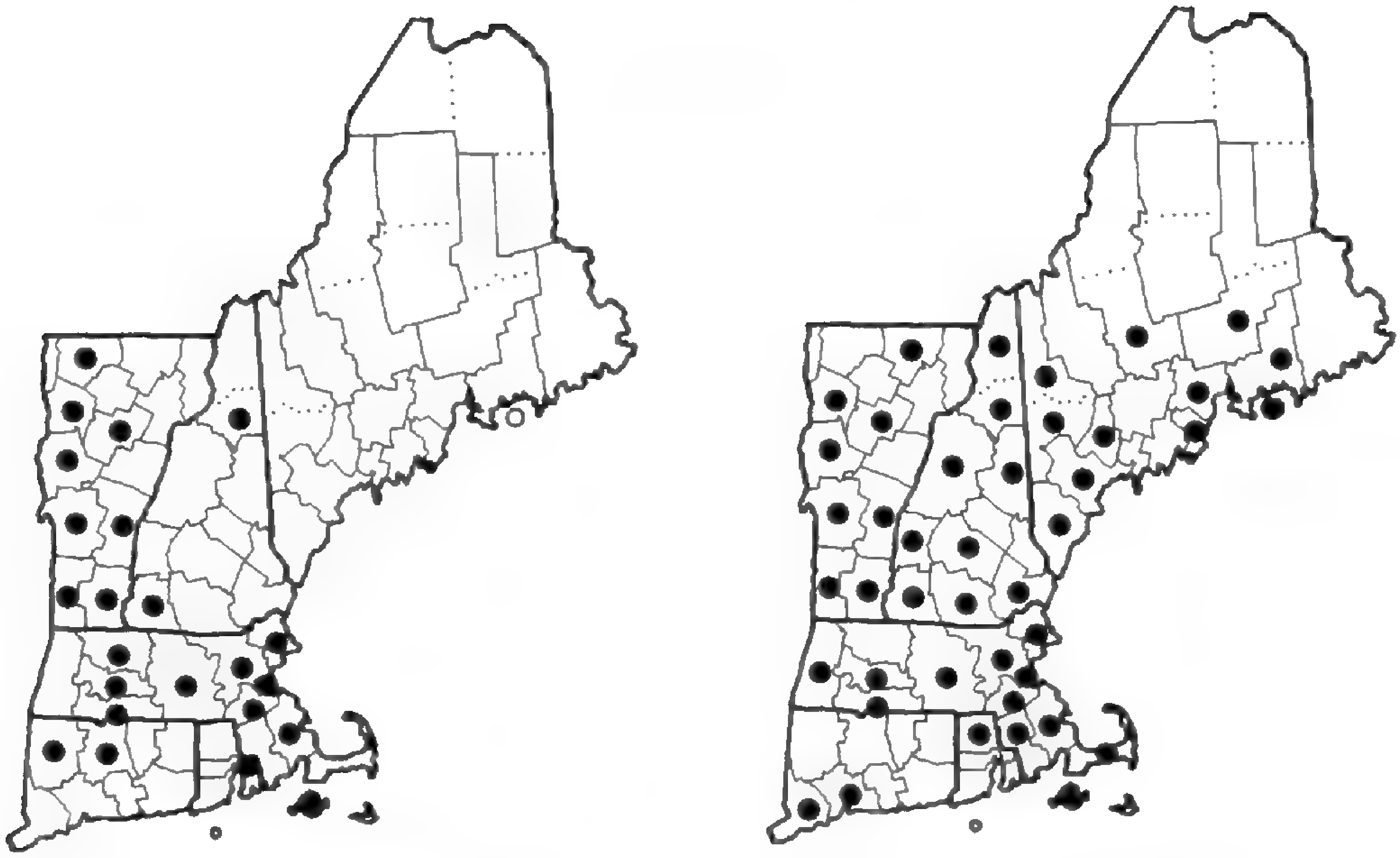


Schizachyrium scoparium

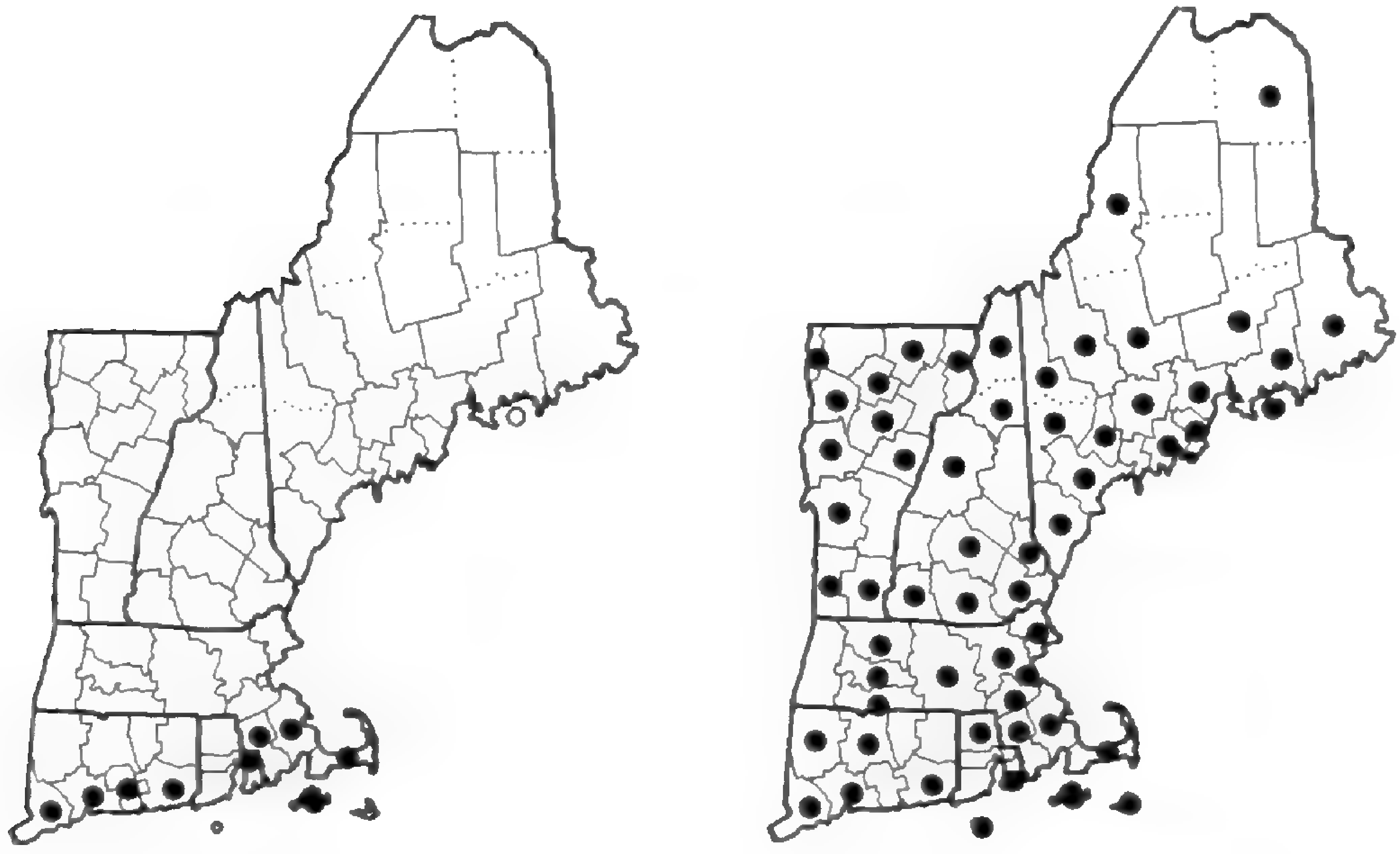


SECALE CEREALE

Figure 74. Distribution maps for *Schizachne purpurascens, Schizachyrium littorale, S. scoparium* and *SECALE CEREALE.*

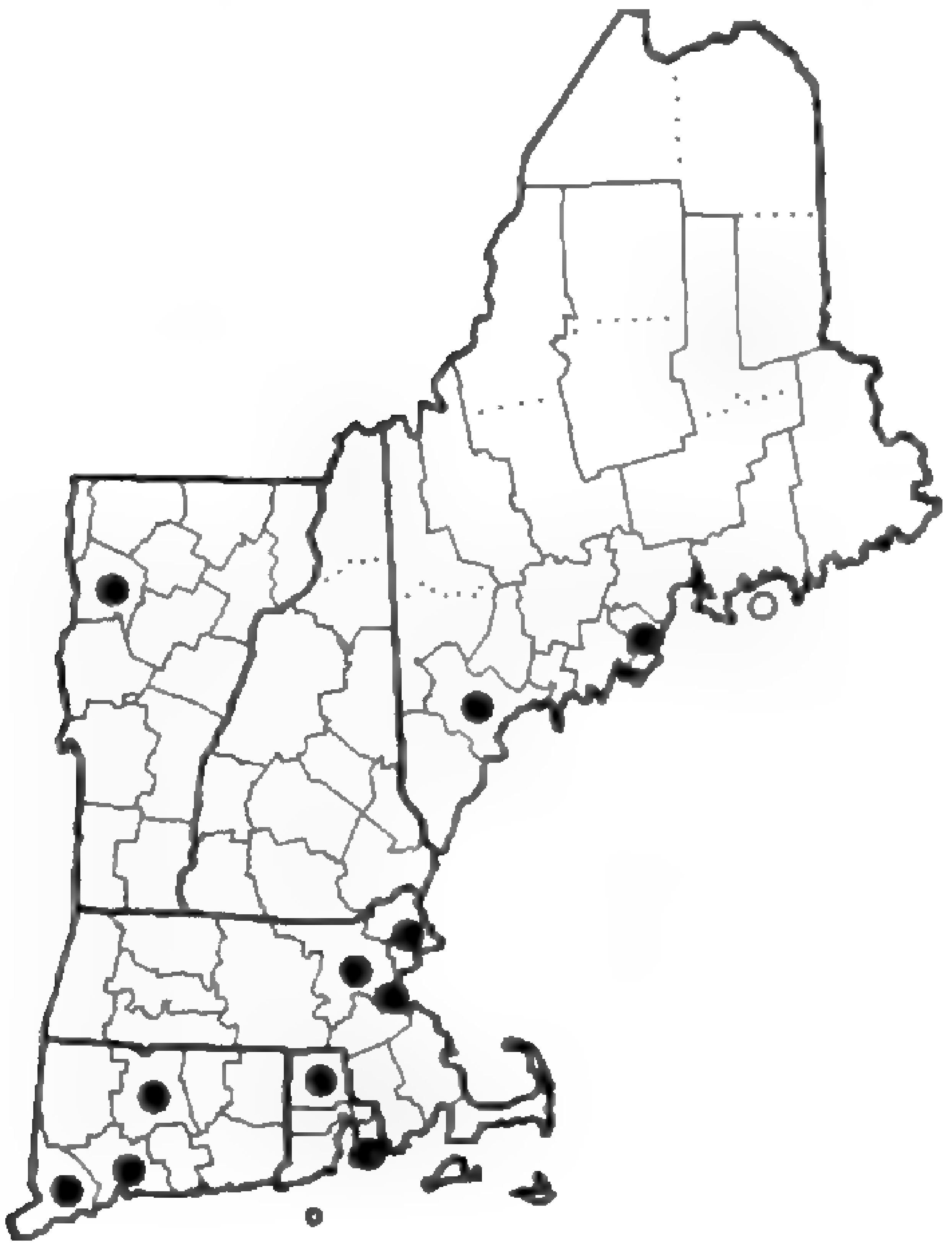


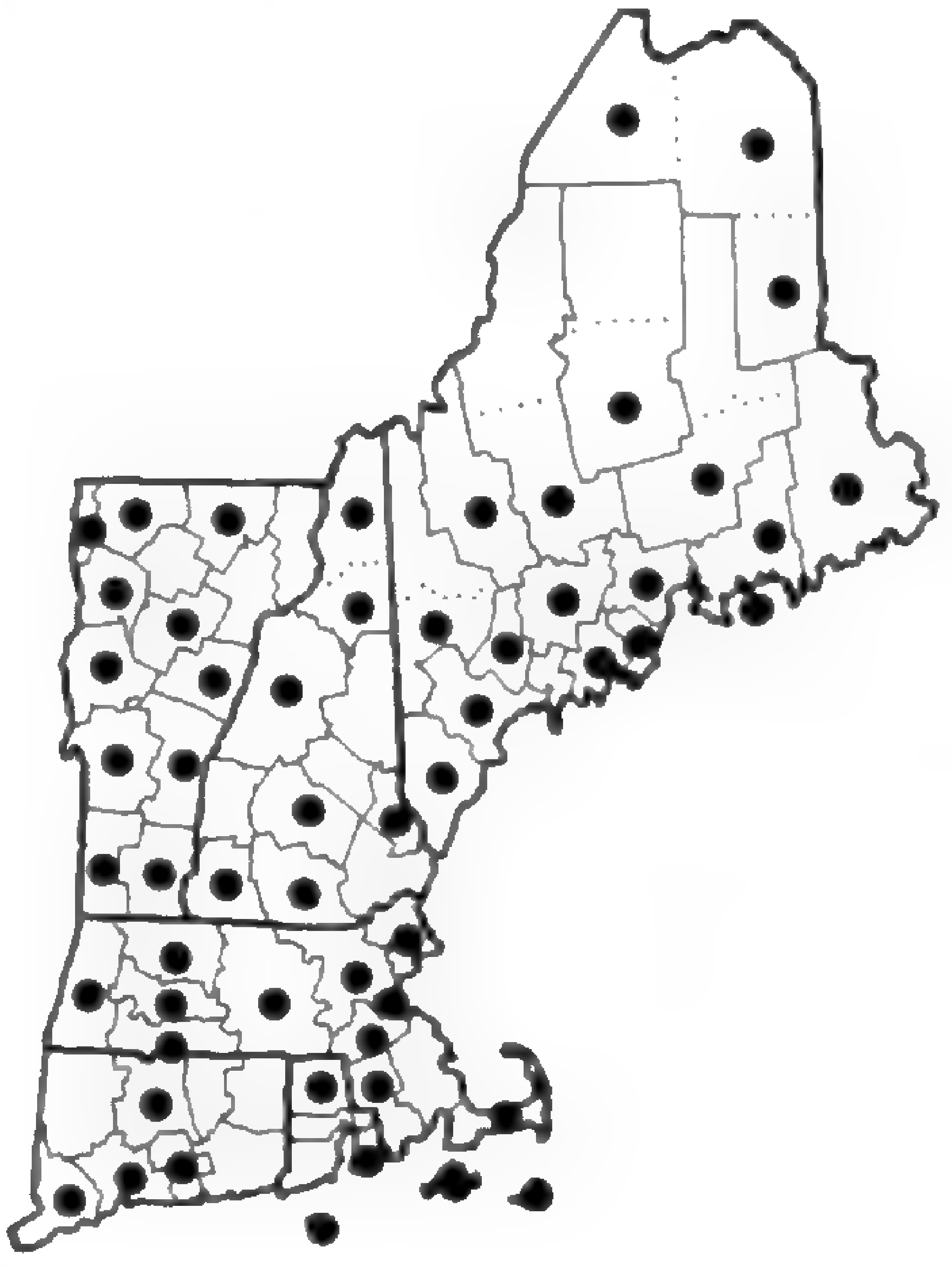
SETARIA FABERI *SETARIA ITALICA*



Setaria parviflora *SETARIA PUMILA*

Figure 75. Distribution maps for *SETARIA FABERI*, *S. ITALICA*, *S. parviflora* and *S. PUMILA*.





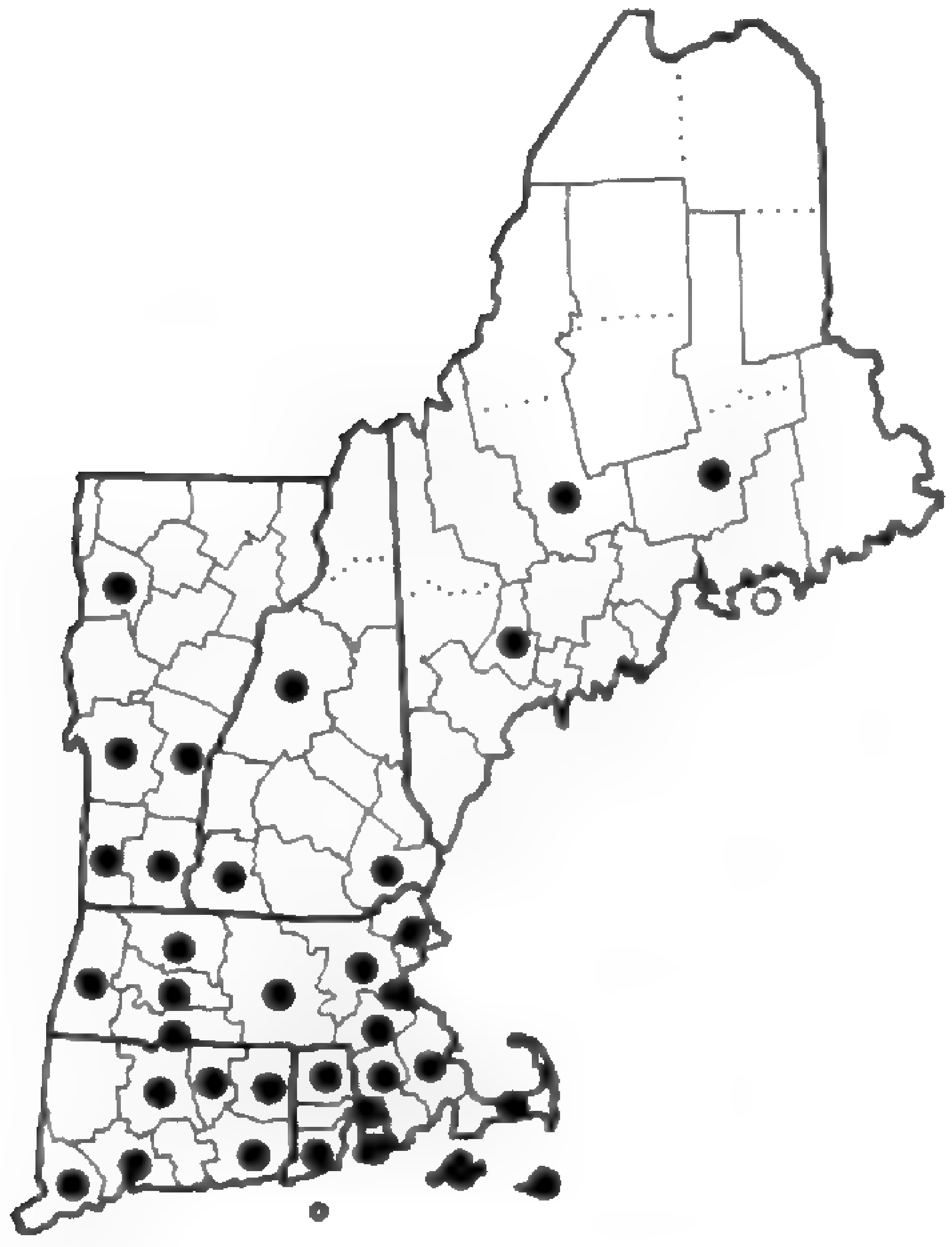
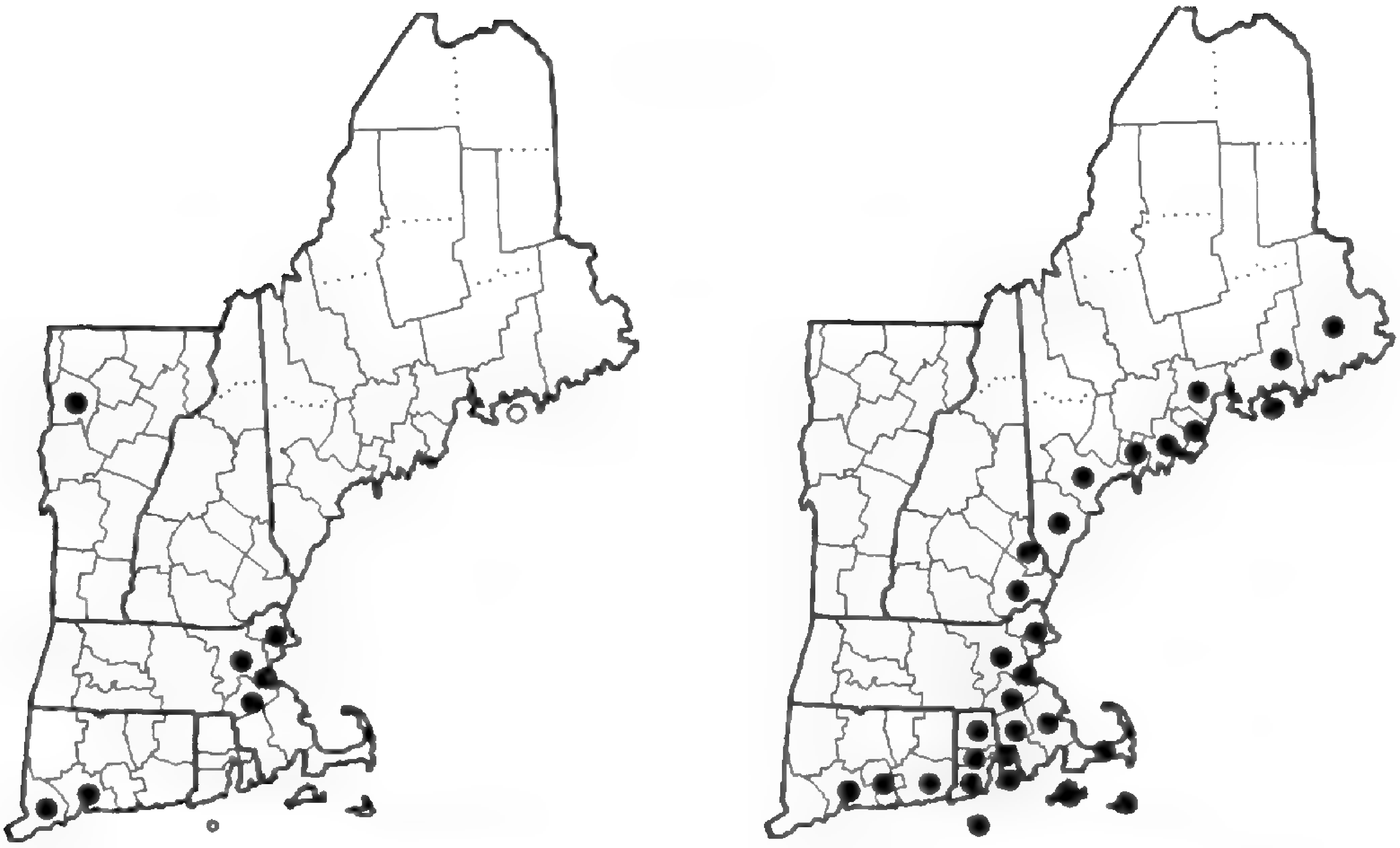
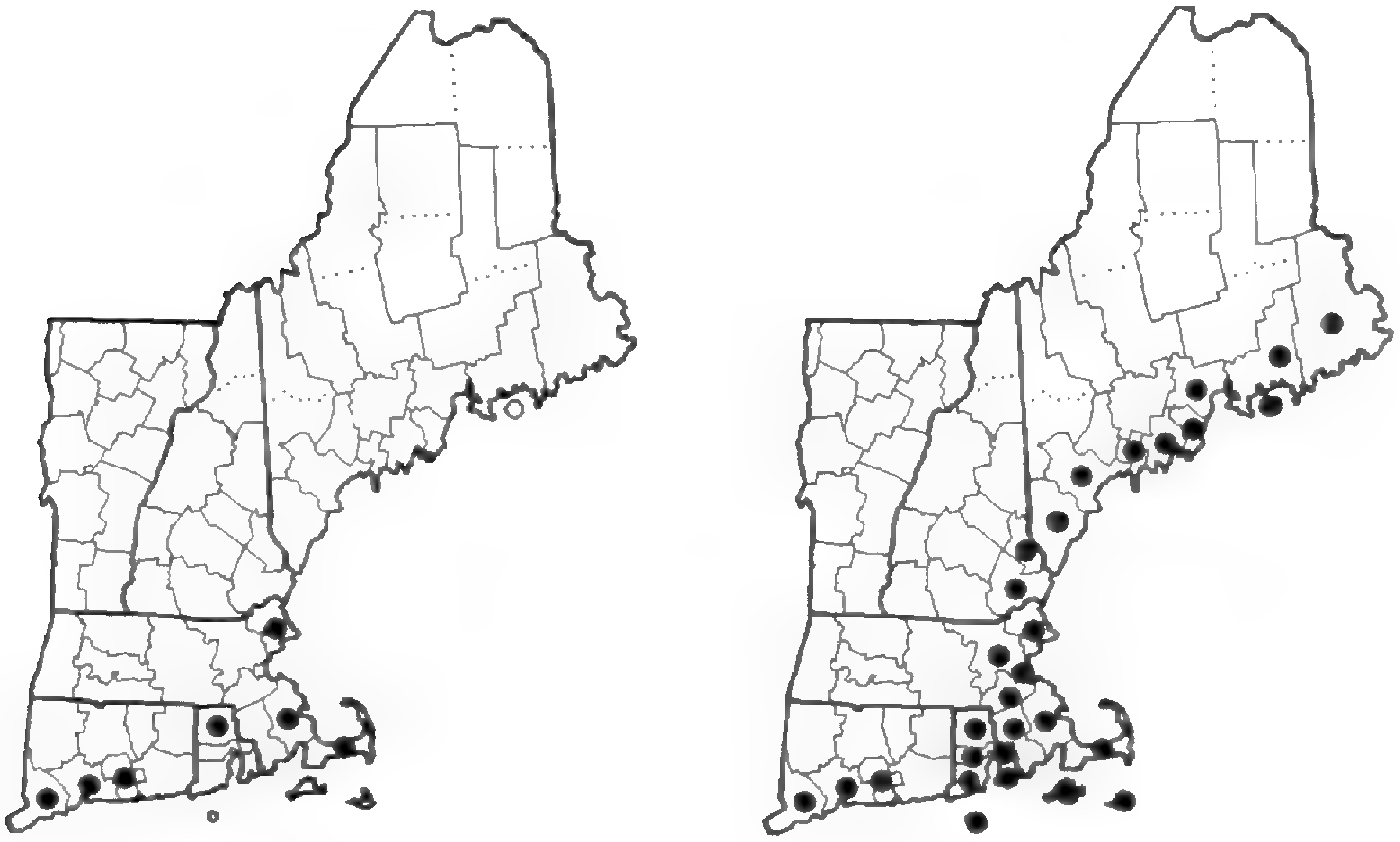


Figure 76. Distribution maps for *SETARIA VERTICILLATA, S. VIRIDIS, Sorghastrum nutans* and *SORGHUM BICOLOR.*

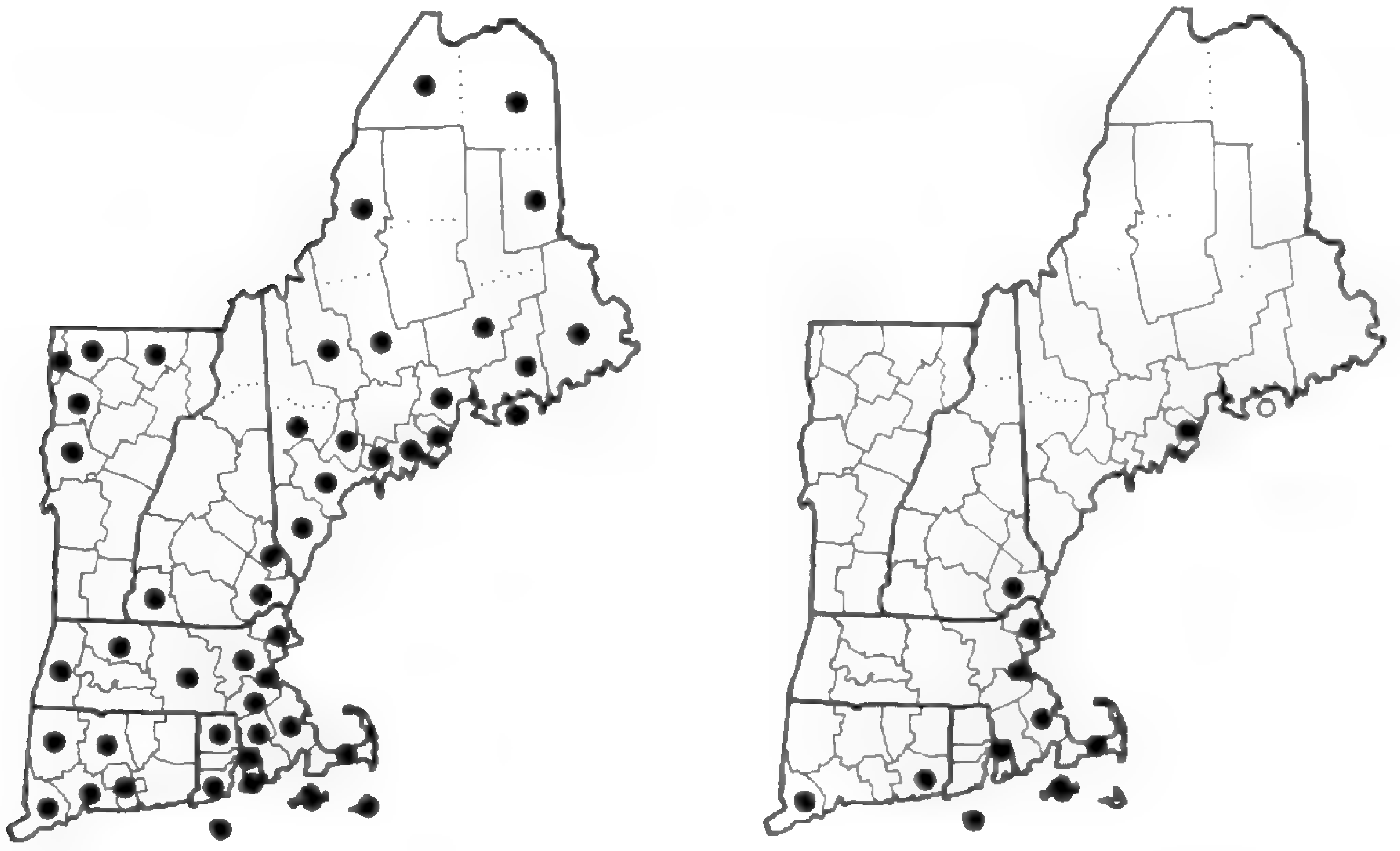


SORGHUM HALEPENSE *Spartina alterniflora*



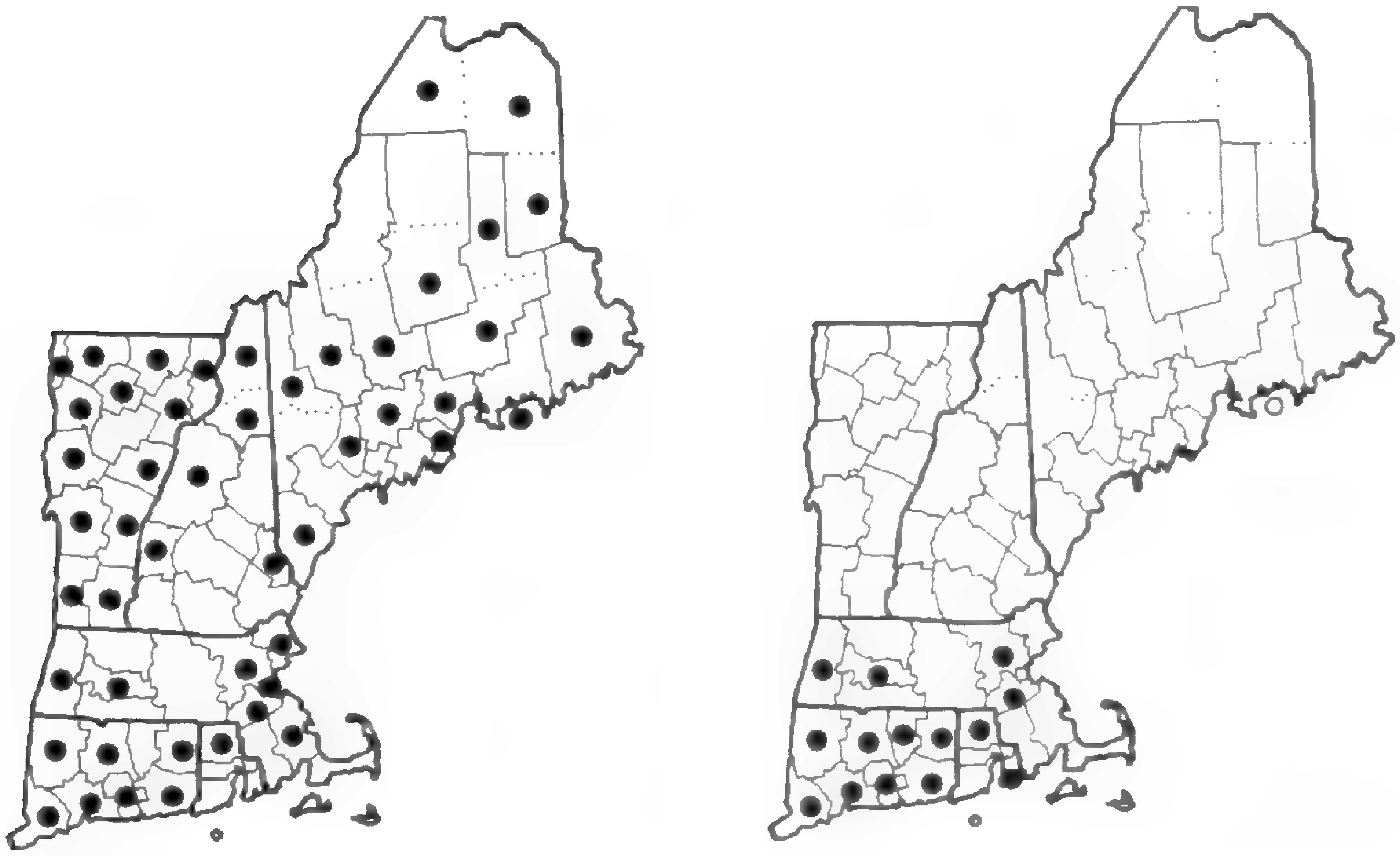
Spartina cynosuroides *Spartina patens*

Figure 77. Distribution maps for *SORGHUM HALEPENSE*, *Spartina alterniflora*, *S. cynosuroides* and *S. patens*.



Spartina pectinata

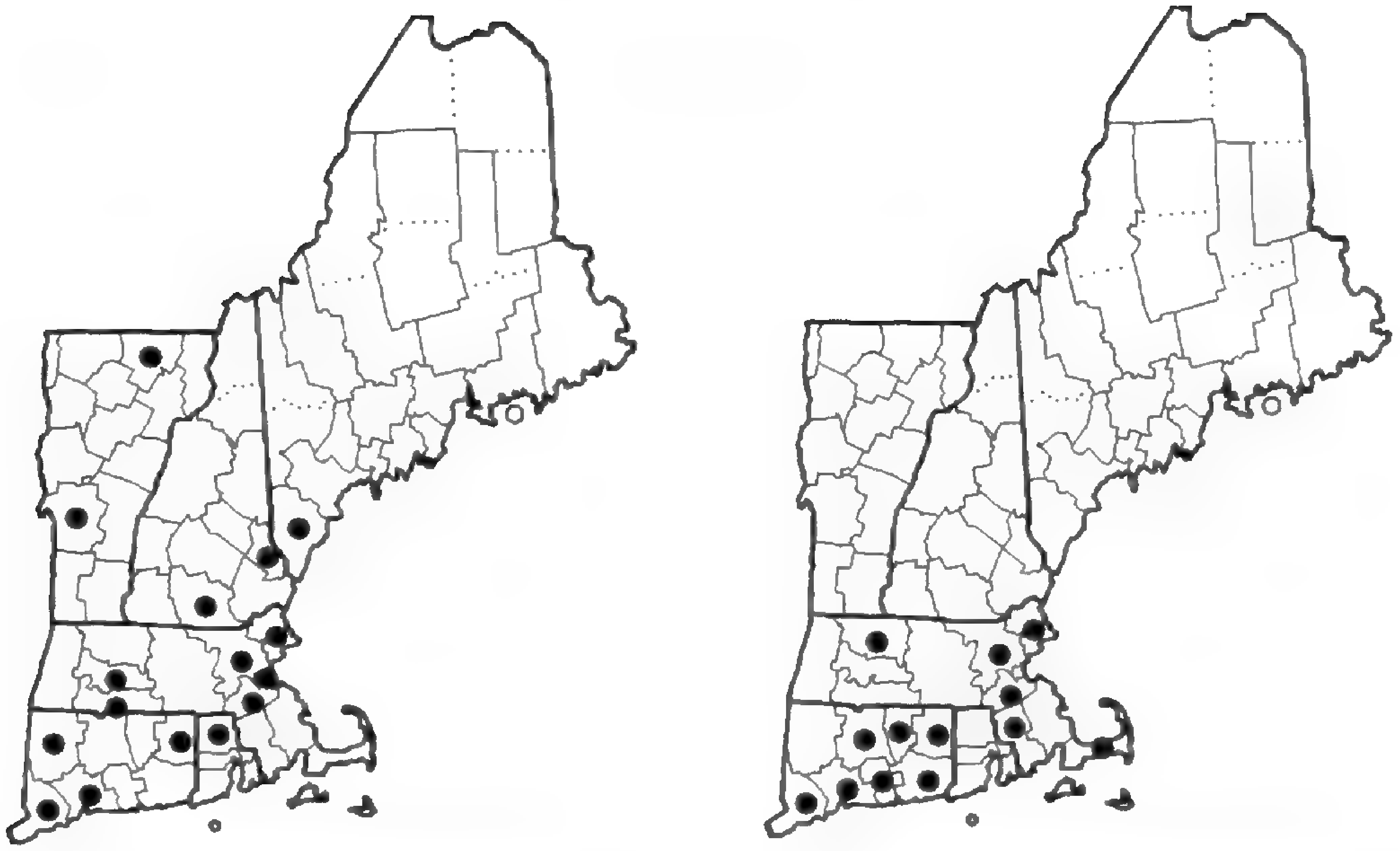
Spartina x *caespitosa*



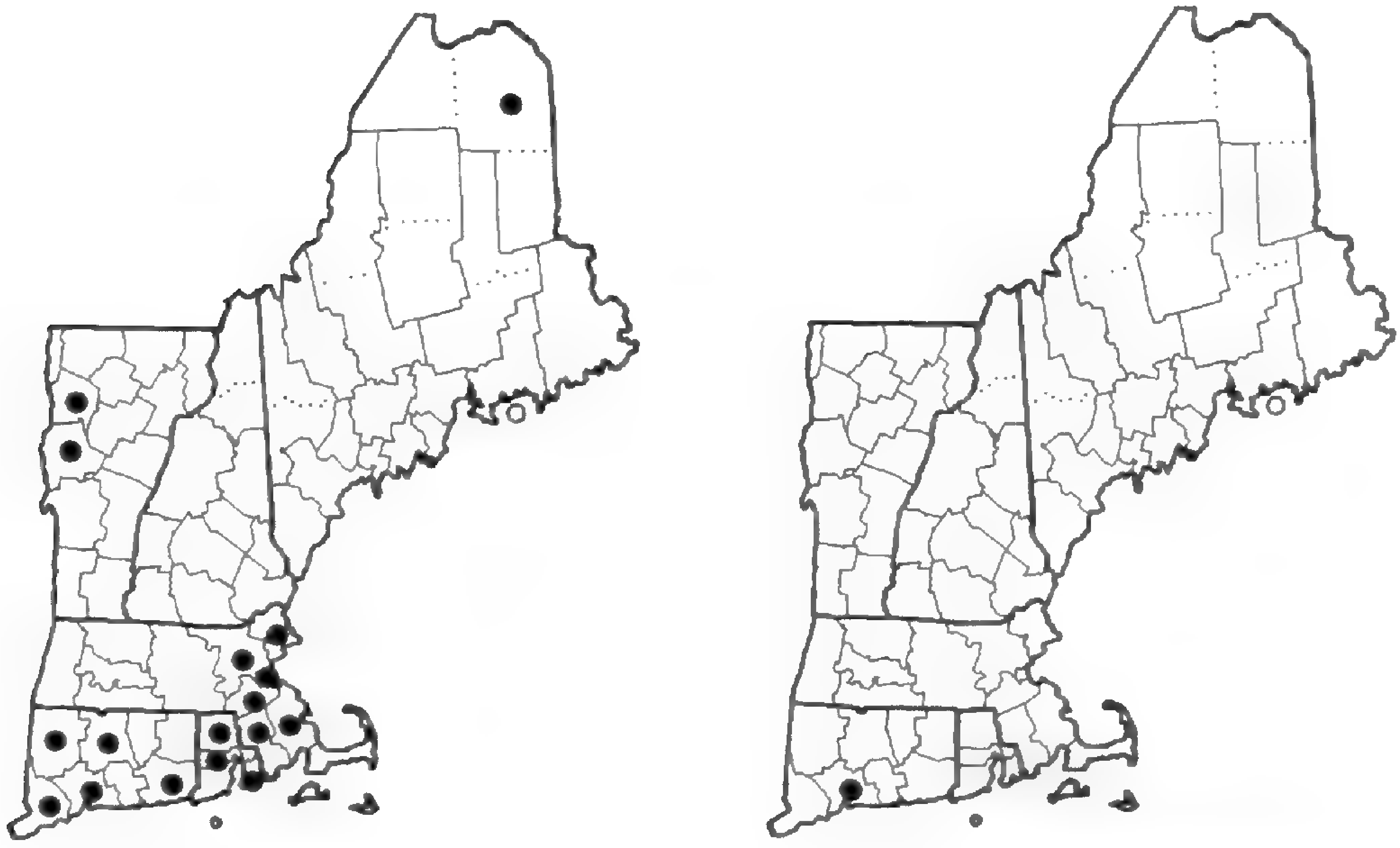
Sphenopholis intermedia

Sphenopholis nitida

Figure 78. Distribution maps for *Spartina pectinata*, *S.* × *caespitosa*, *Sphenopholis intermedia* and *S. nitida*.

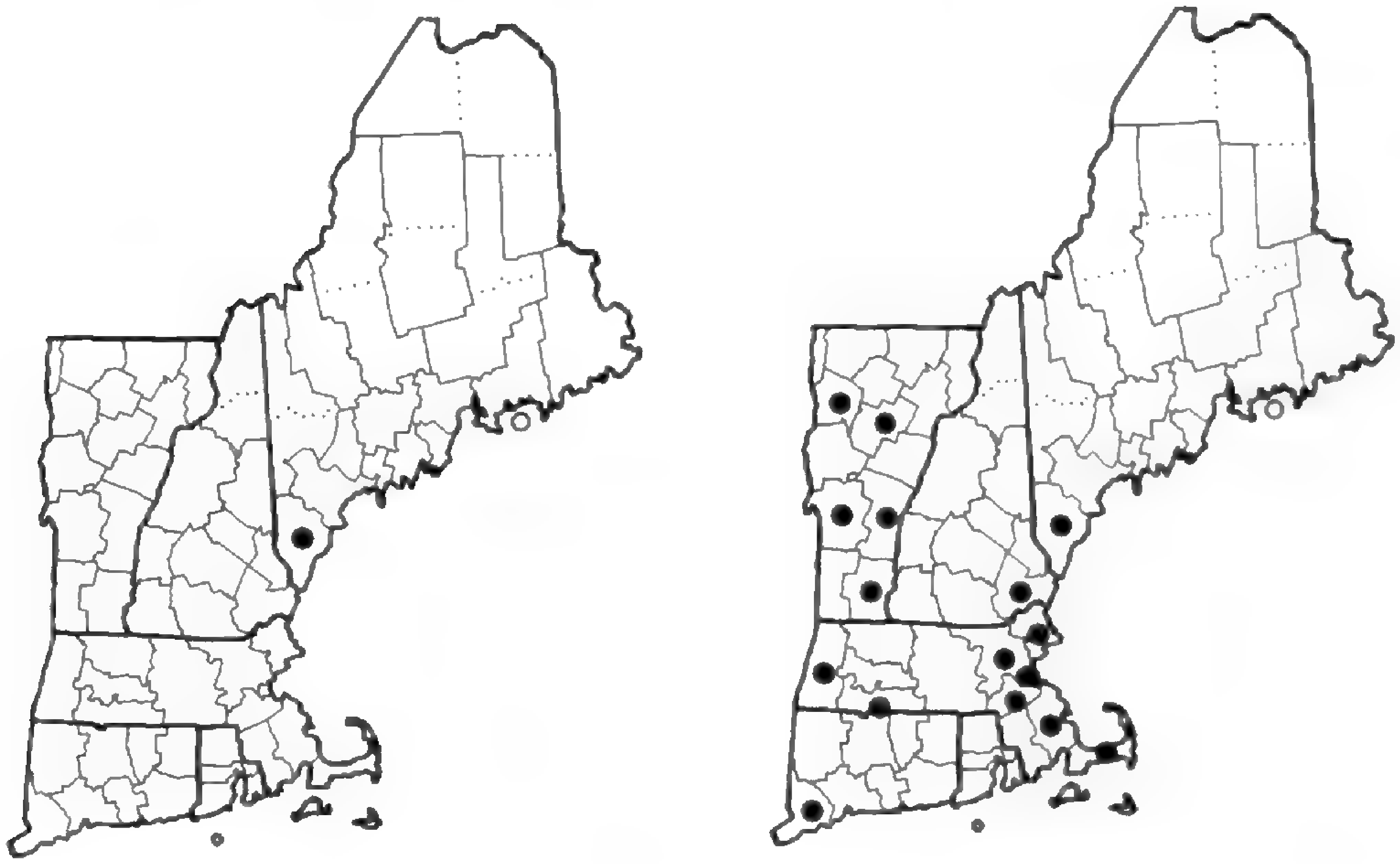


Sphenopholis obtusata *Sphenopholis pensylvanica*



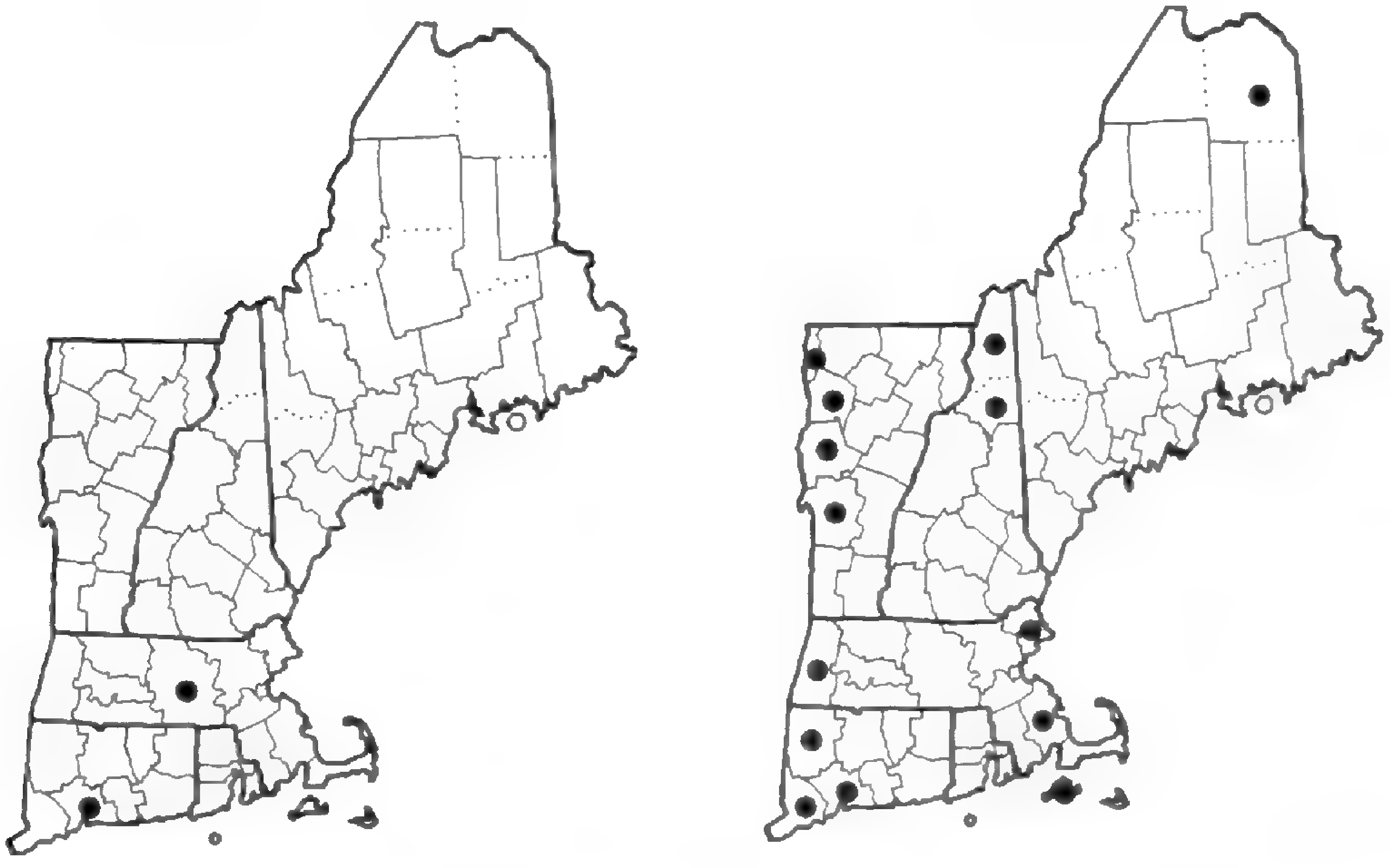
Sporobolus asper *Sporobolus clandestinus*

Figure 79. Distribution maps for *Sphenopholis obtusata, S. pensylvanica, Sporobolus asper* and *S. clandestinus.*



SPOROBOLUS CONTRACTUS

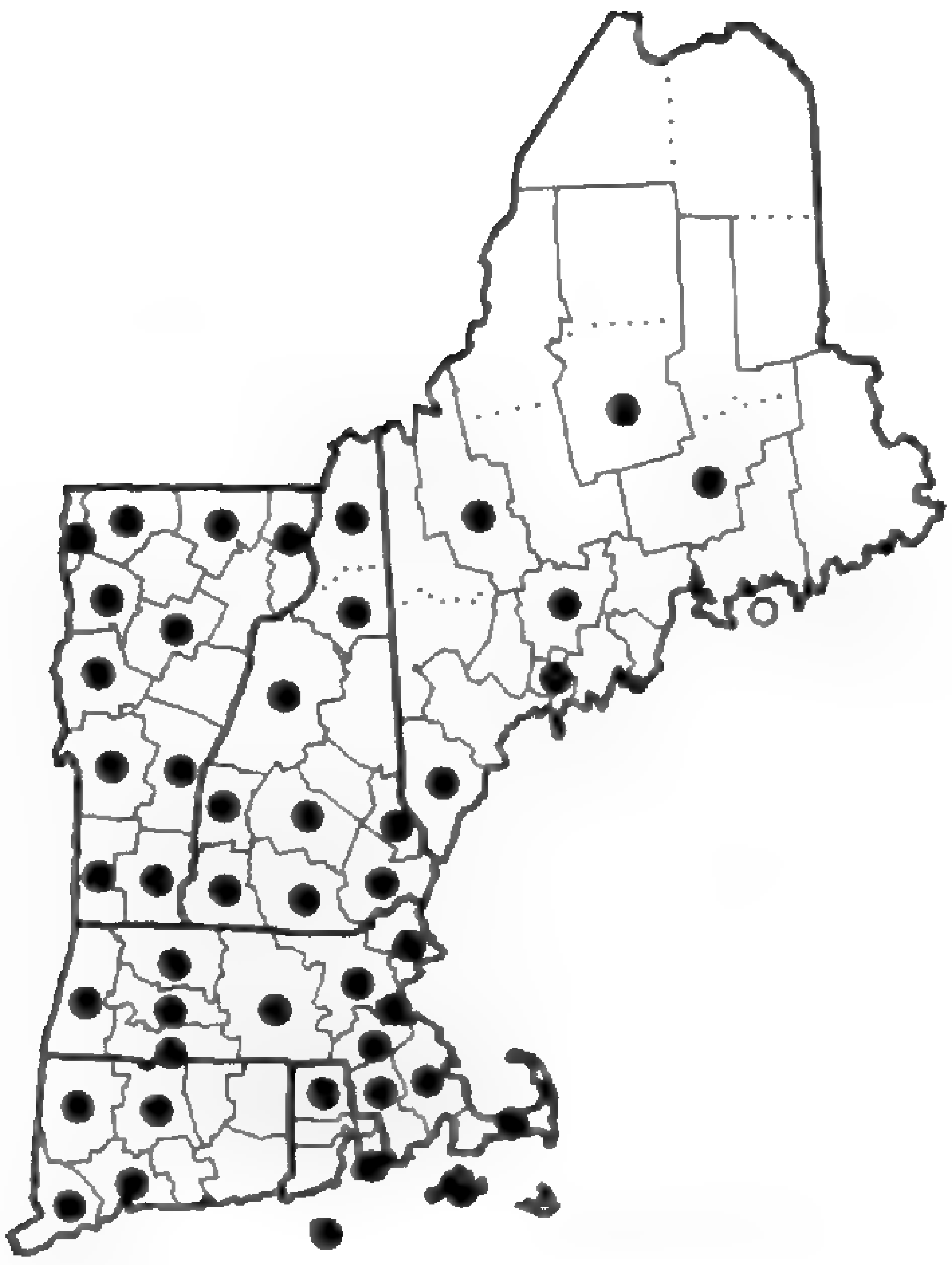
Sporobolus cryptandrus



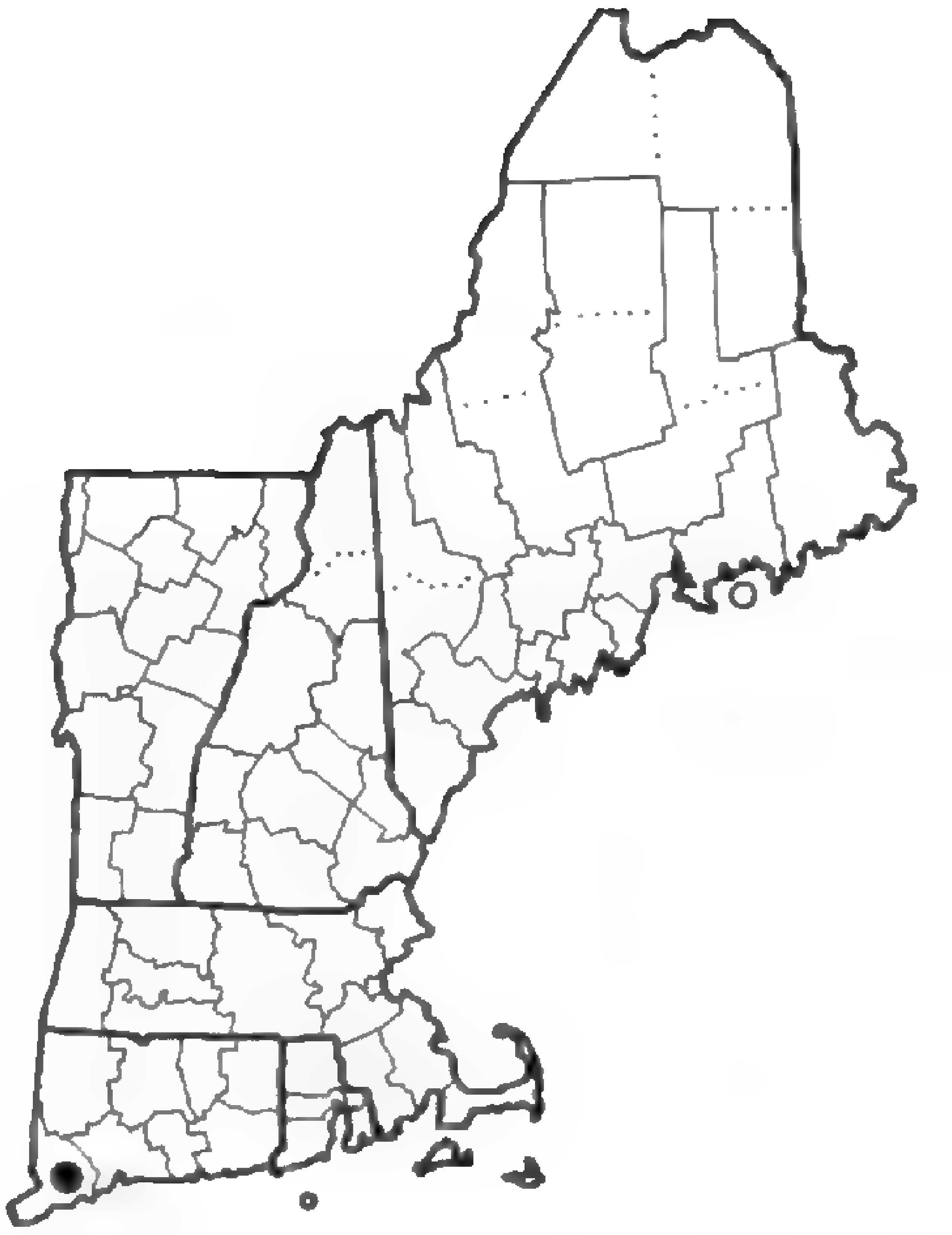
Sporobolus heterolepis

Sporobolus neglectus

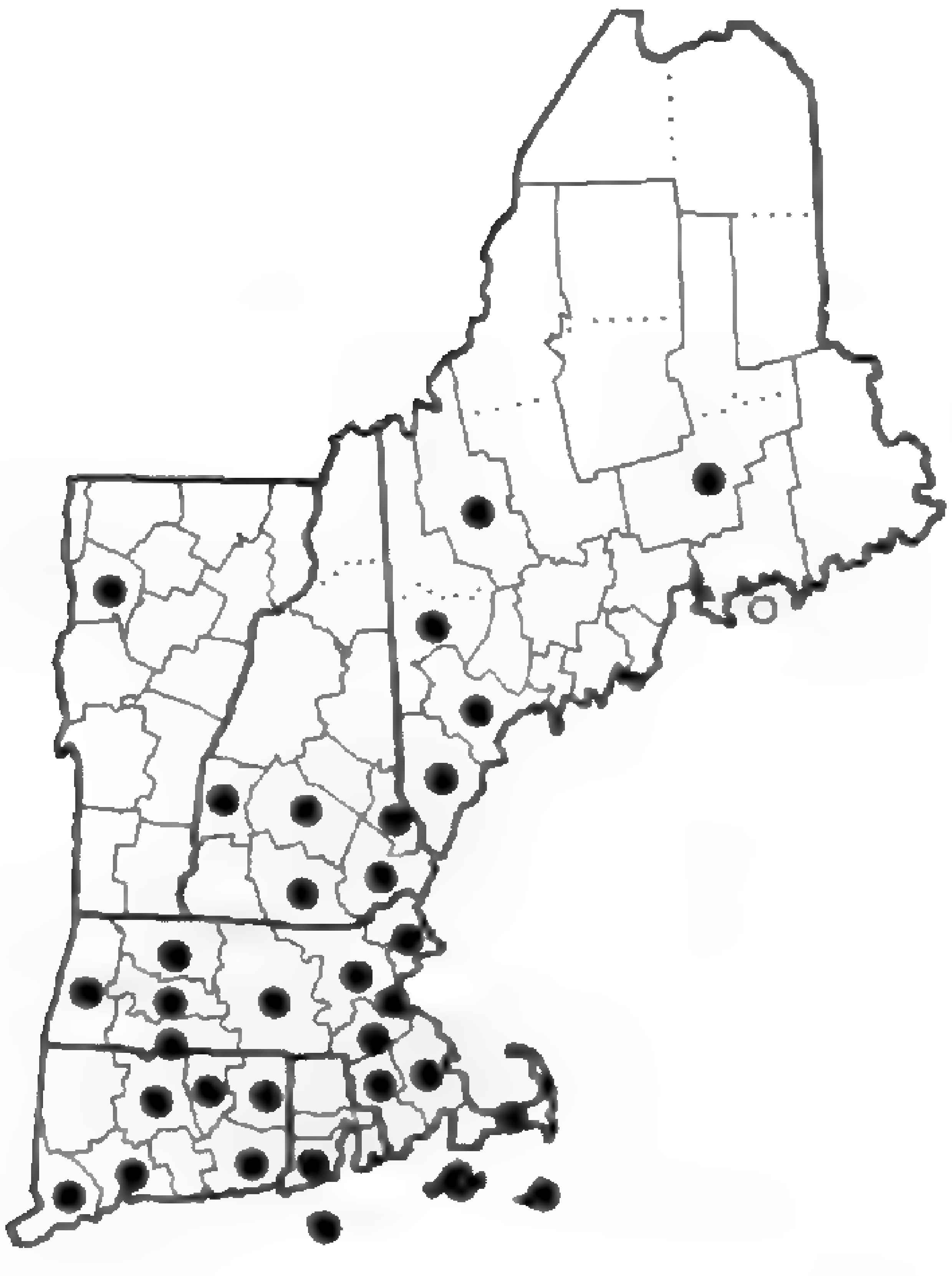
Figure 80. Distribution maps for *SPOROBOLUS CONTRACTUS*, *S. cryptandrus*, *S. heterolepis* and *S. neglectus*.



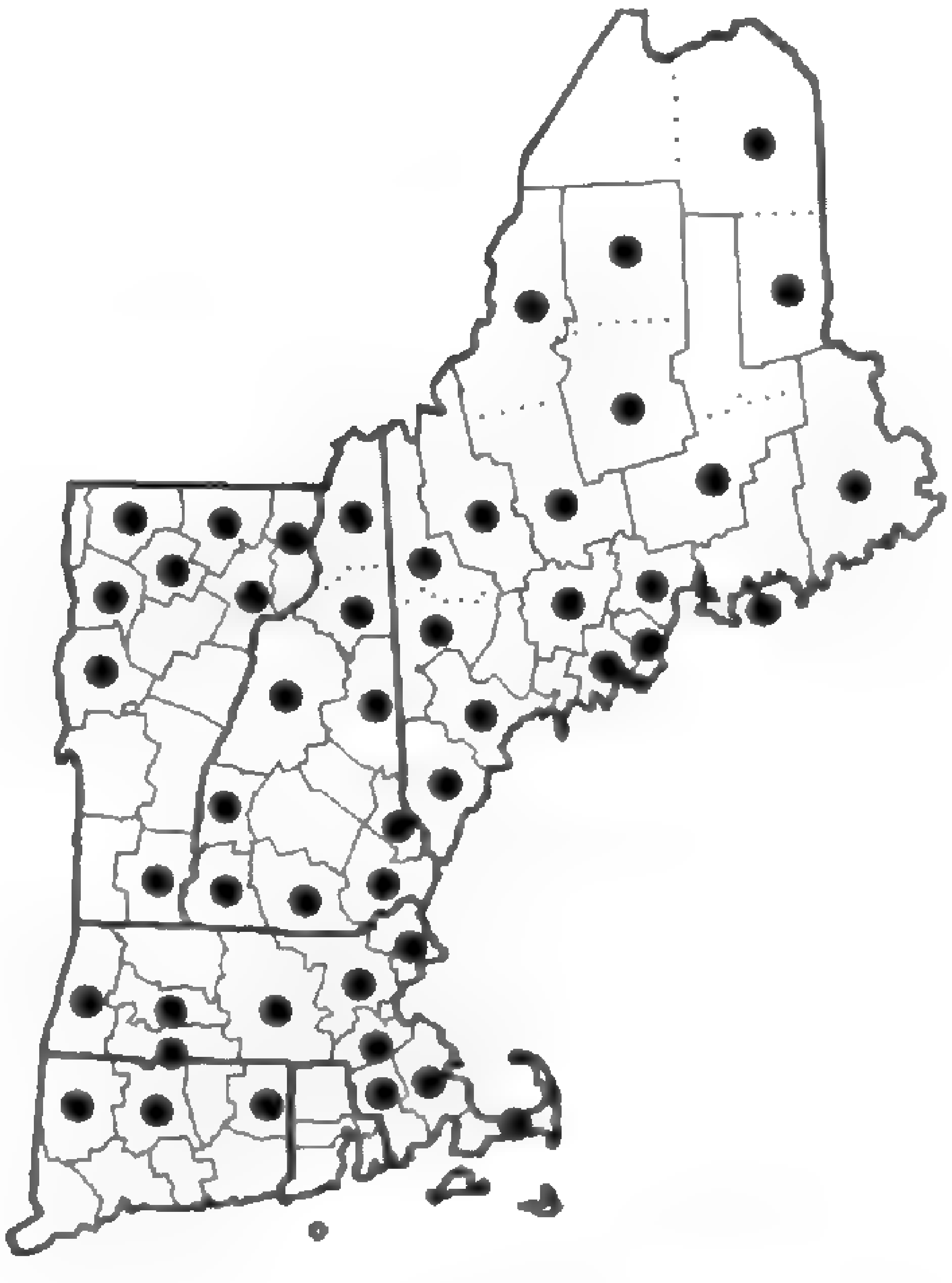
Sporobolus vaginiflorus



TAENIATHERUM CAPUT-MEDUSAE

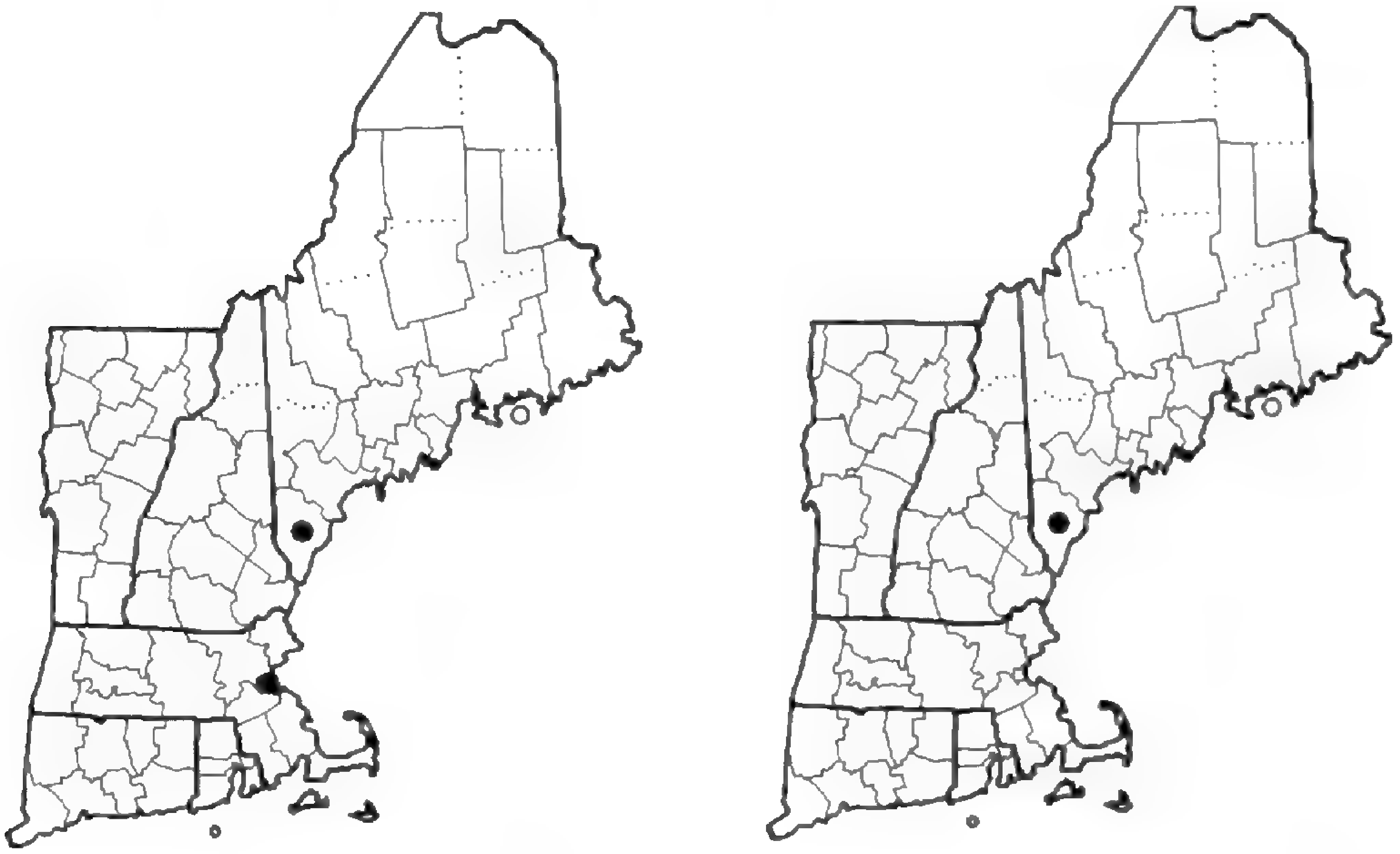


Torreyochloa pallida
var. *pallida*



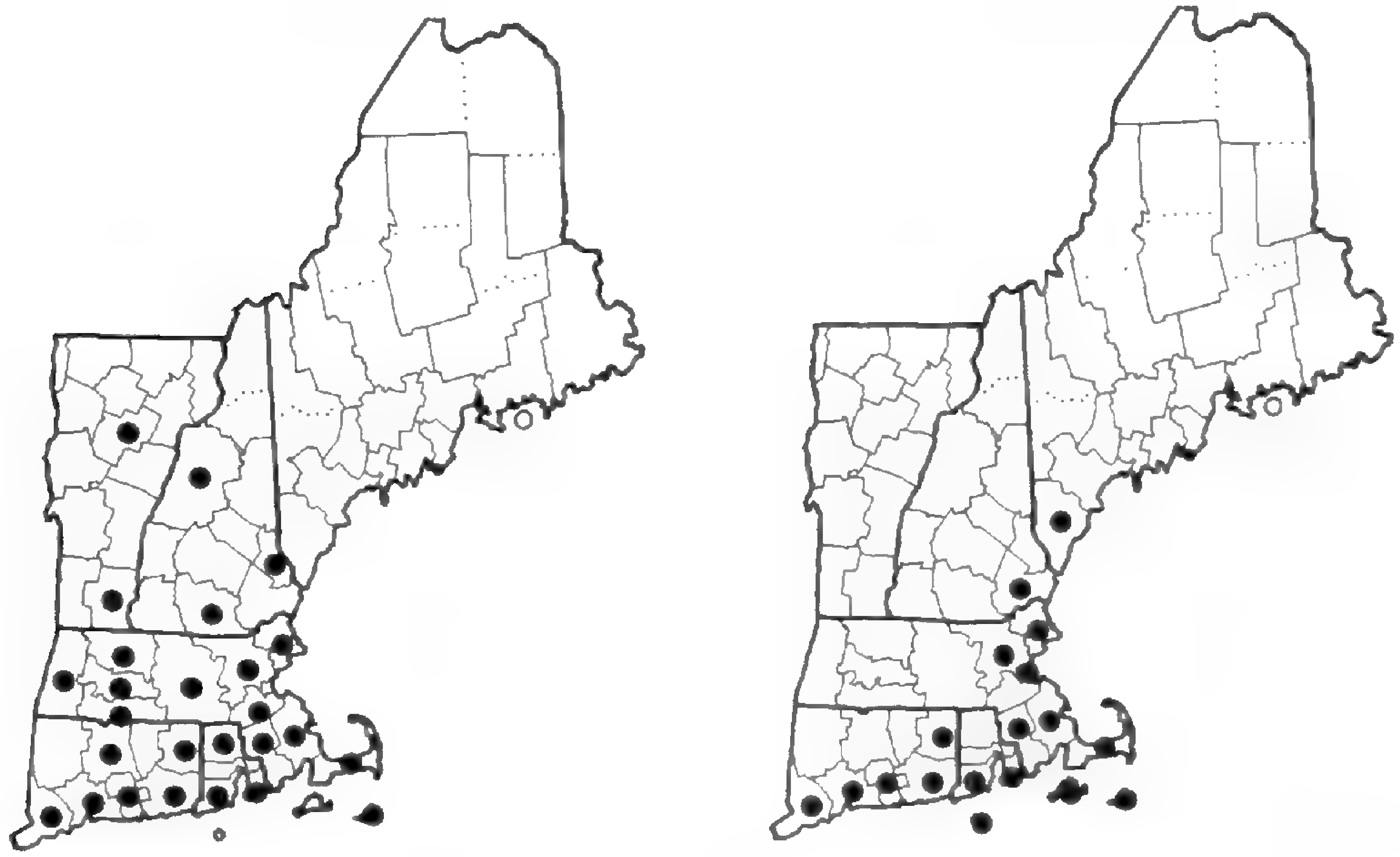
Torreyochloa pallida
var. *fernaldii*

Figure 81. Distribution maps for *Sporobolus vaginiflorus, TAENIATHERUM CAPUT-MEDUSAE, Torreyochloa pallida* var. *pallida* and *T. pallida* var. *fernaldii.*



TRAGUS BERTERONIANUS

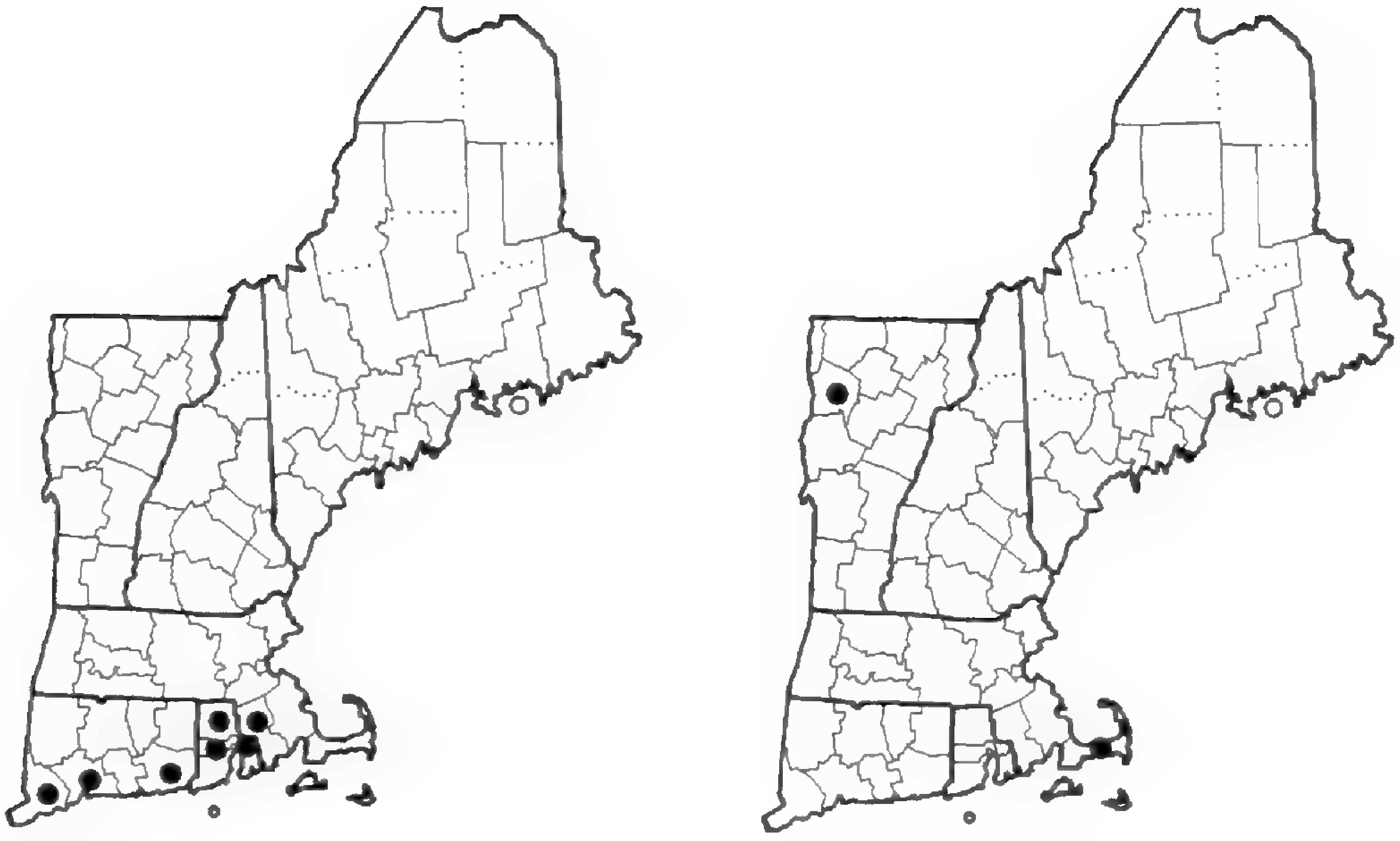
TRAGUS RACEMOSUS



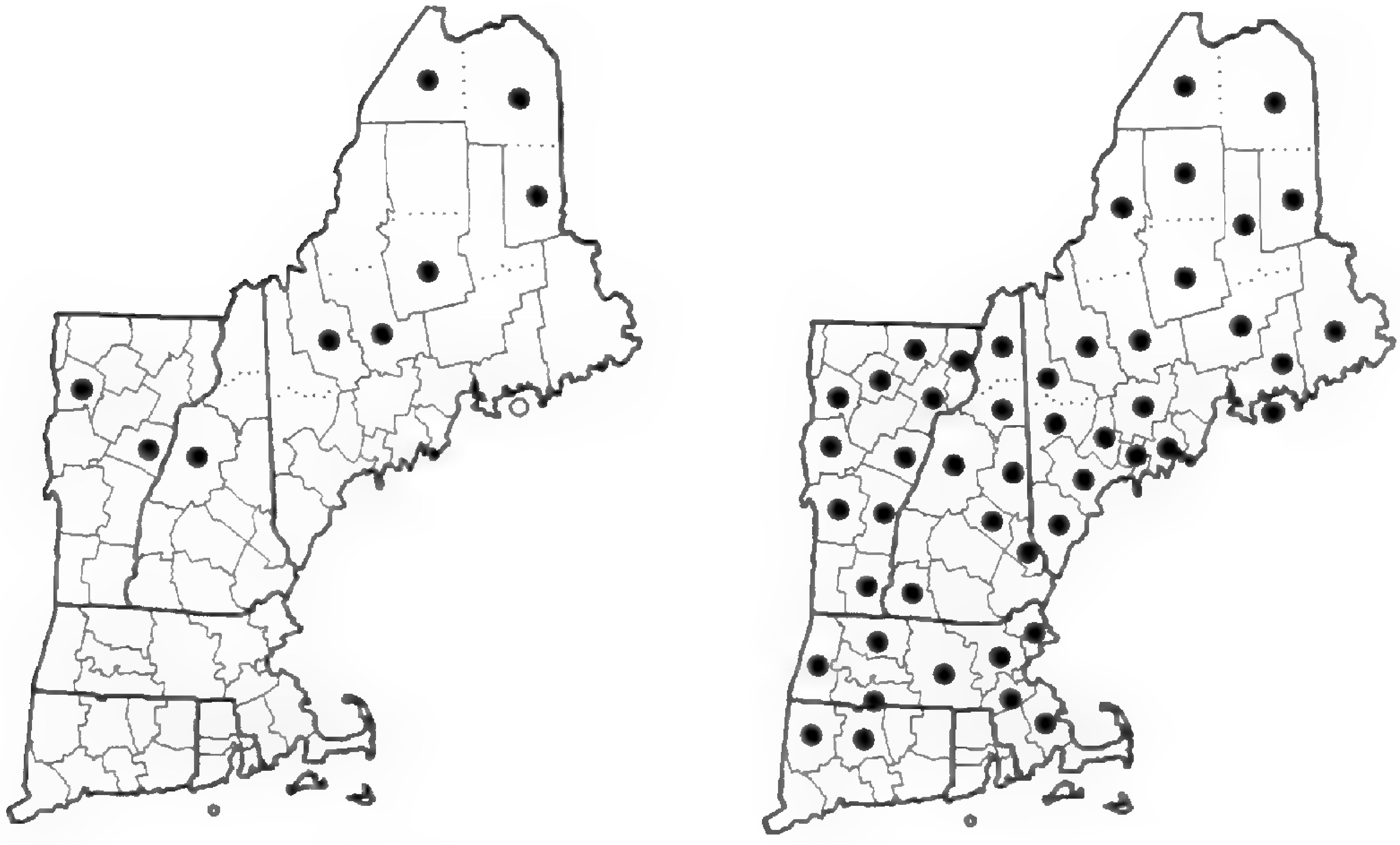
Tridens flavus

Triplasis purpurea

Figure 82. Distribution maps for *TRAGUS BERTERONIANUS*, *TRAGUS RACEMOSUS*, *Tridens flavus* and *Triplasis purpurea*.

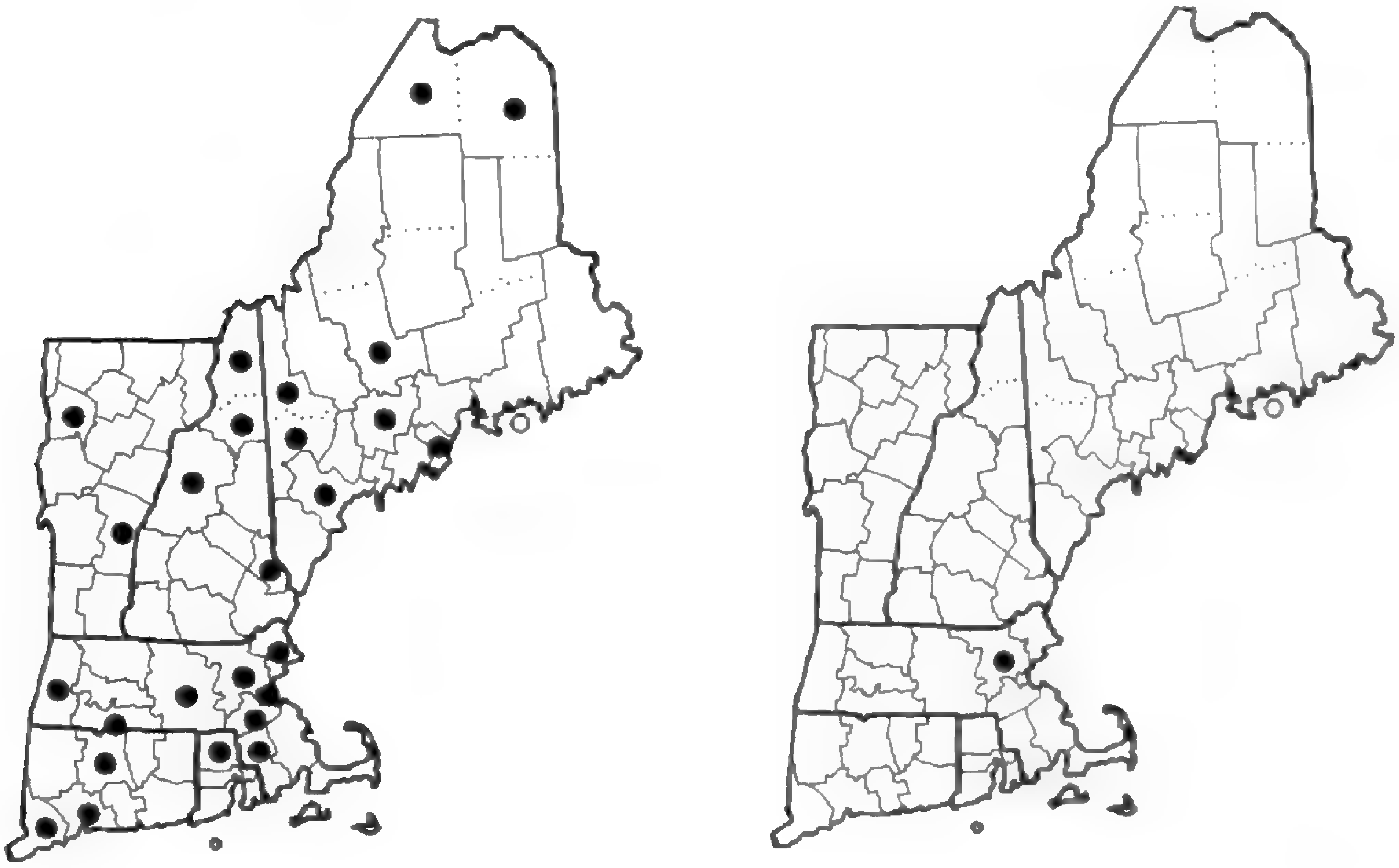


Tripsacum dactyloides *TRISETUM FLAVESCENS*

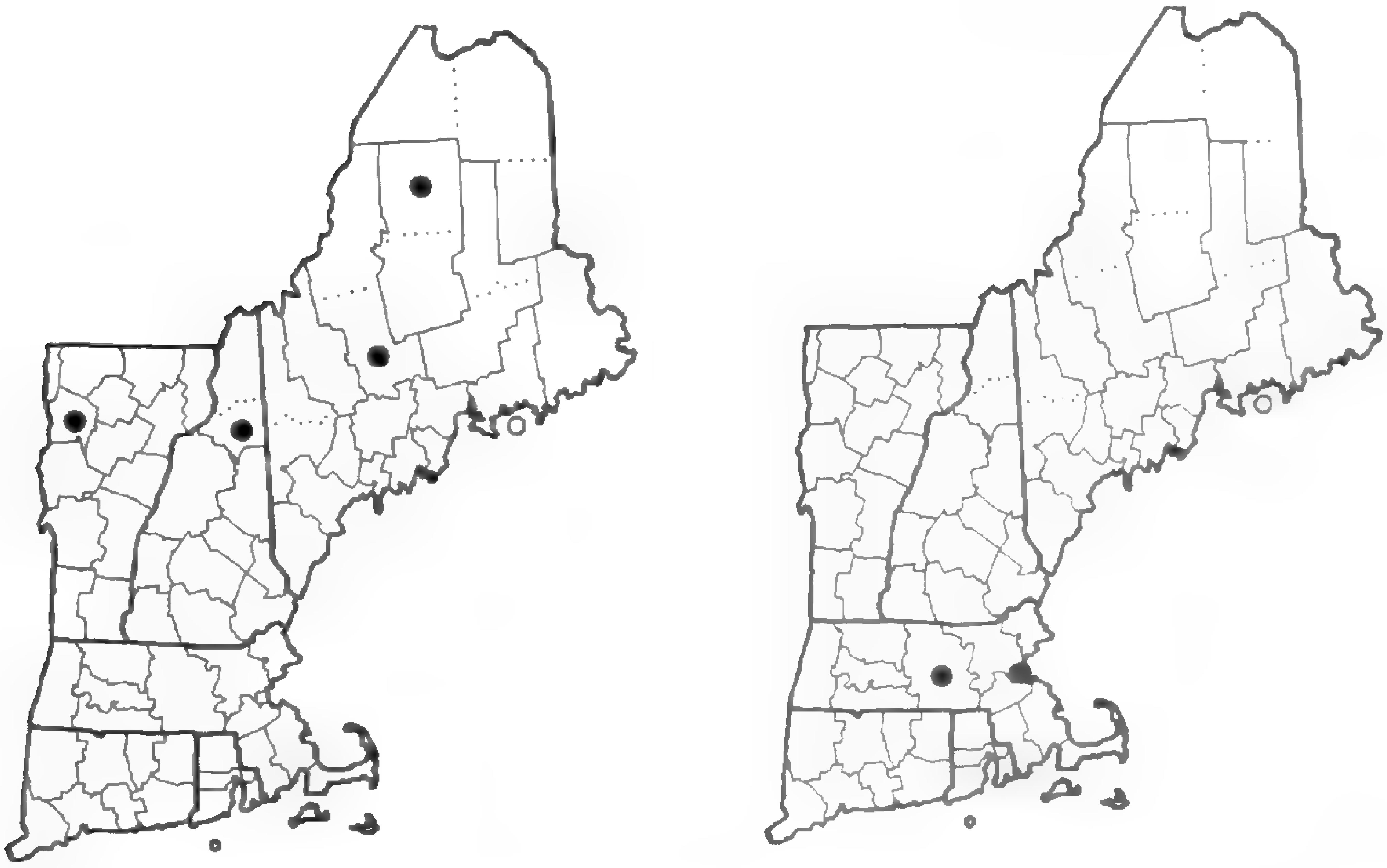


Trisetum melicoides *Trisetum spicatum*

Figure 83. Distribution maps for *Tripsacum dactyloides, TRISETUM FLAVESCENS, T. melicoides* and *T. spicatum.*

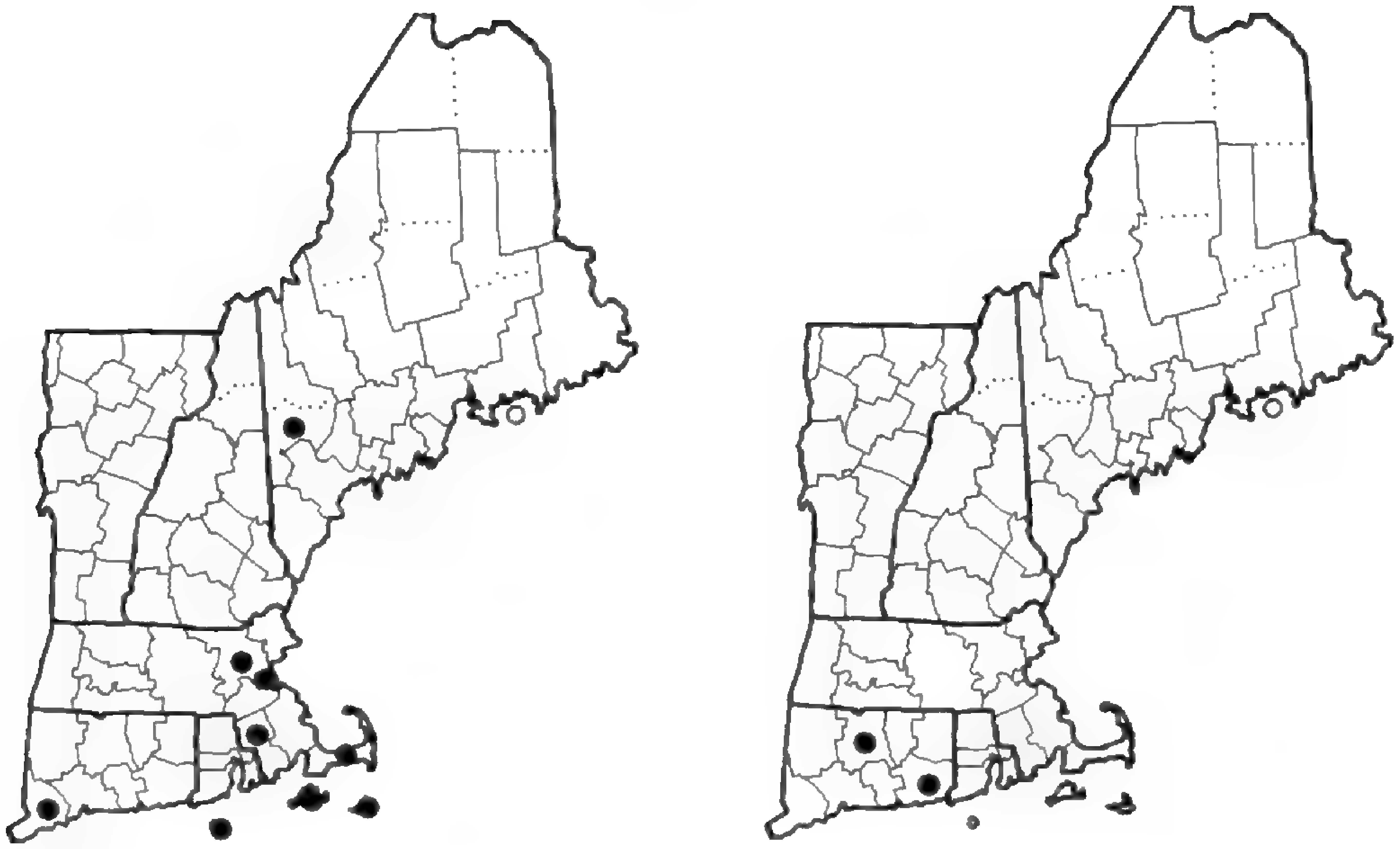


TRITICUM AESTIVUM *UROCHLOA TEXANA*



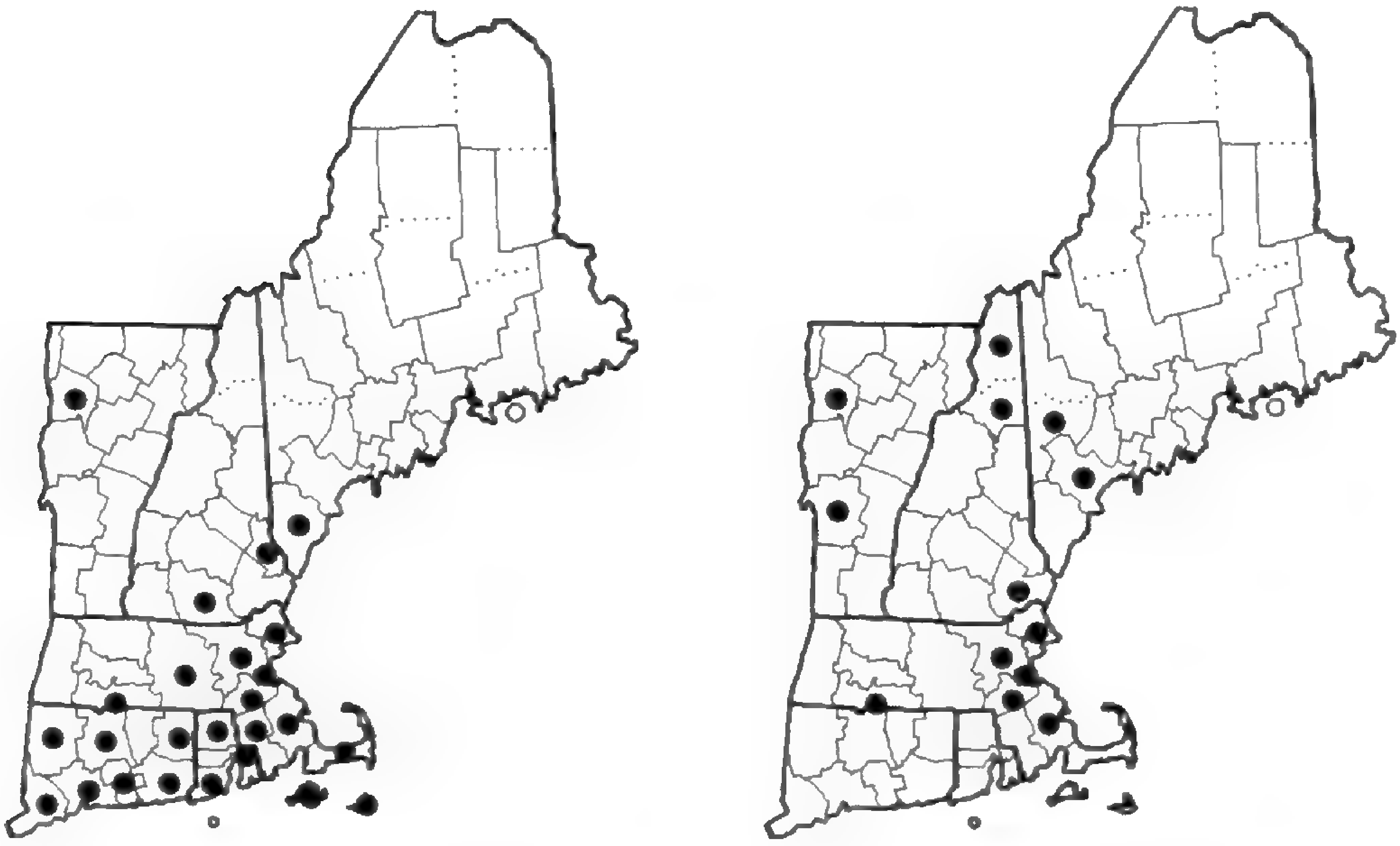
Vahlodea atropurpurea *VULPIA BROMOIDES*

Figure 84. Distribution maps for *TRITICUM AESTIVUM, UROCHLOA TEXANA, Vahlodea atropurpurea* and *VULPIA BROMOIDES.*



VULPIA MYUROS

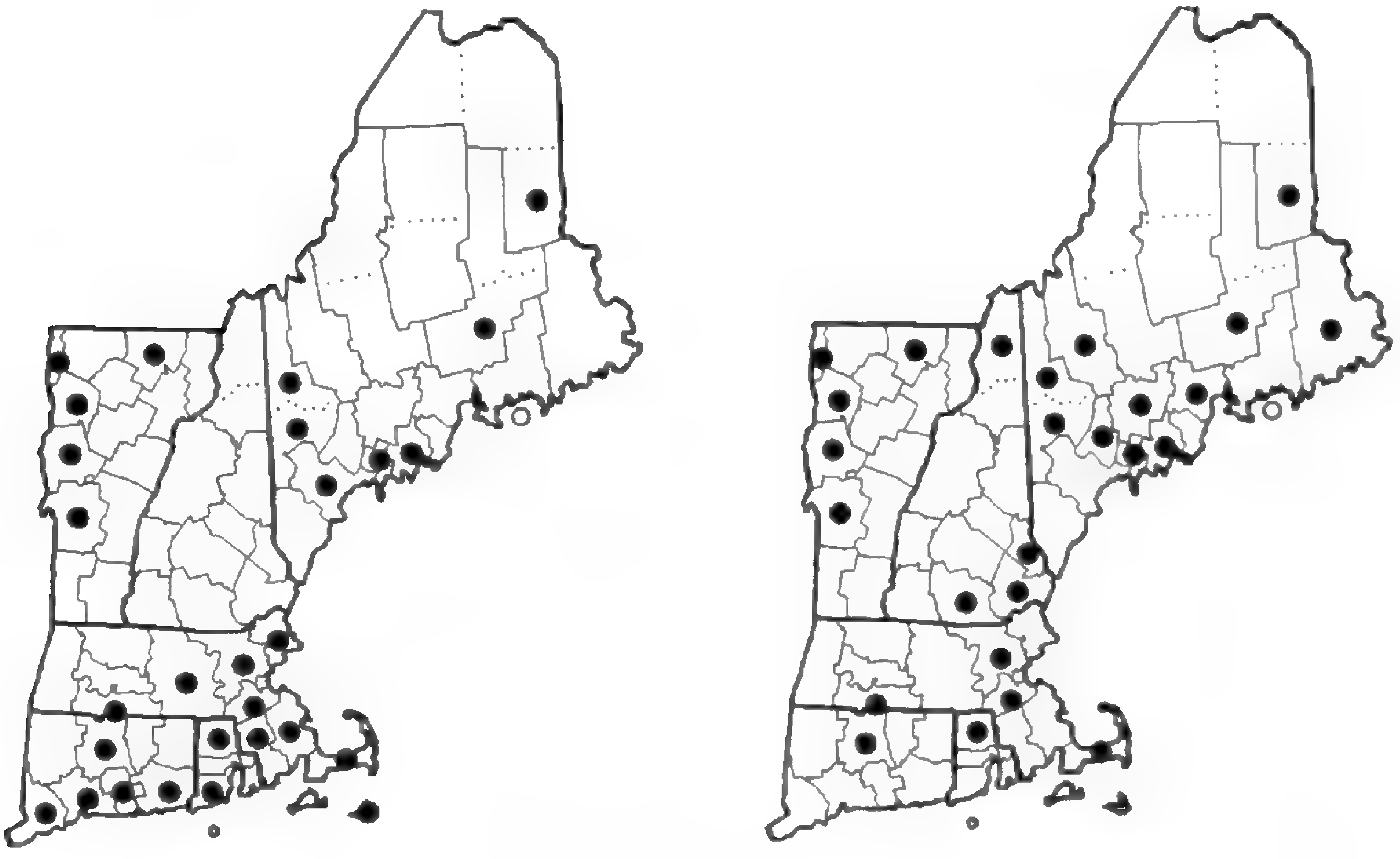
Vulpia octoflora var. *octoflora*



Vulpia octoflora var. *glauca*

ZEA MAYS

Figure 85. Distribution maps for *VULPIA MYUROS*, *V. octoflora* var. *octoflora*, *V. octoflora* var. *glauca* and *ZEA MAYS*.



Zizania aquatica *Zizania palustris*

Figure 86. Distribution maps for *Zizania aquatica* and *Z. palustris.*

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NEBC MEETING NEWS

March 1998. Outgoing Club President Don Hudson, President of the Chewonki Foundation, spoke on "The New Natural History: A Naturalist's Perspective on Science Education." The topic was selected to provide insight into his working life as a naturalist and into his personal philosophy of learning and teaching, which stems from Don's concern that students and the general public are poorly prepared to solve problems, address issues of ecology and the landscape, or contribute to discussions of public policy and stewardship of natural resources.

From his perspective as a teacher and lifelong student of natural history, Don shared his four "lessons" for teaching: (1) A sense of place is essential to fuel a lifelong passion for learning; (2) Teach what you love, so that your enthusiasm may infect even the most jaded student with passion; (3) The first job of a teacher should be to provide the space and time for unique discovery; and (4) The second job of a teacher should be to provide students with as many opportunities as possible to sort through the strands of our knowledge to find connections.

Don described how his love of science and learning was influenced by teachers and fellow naturalists who provided space, resources, questions, and encouragement, and demonstrated that the energy and enthusiasm of discovery is key to continued involvement and learning. He cited a recent article by E. O. Wilson in the *Atlantic Monthly,* dealing with the increased fragmentation and specialization of the scientific disciplines and the inability of scientists—or the educated public—to find coherence among scientific disciplines or between science and the humanities. Don also quoted William Morton Wheeler's presidential address to the American Society of Naturalists, 75 years ago, in which Wheeler railed against academic "dry rot," which he blamed on narrow specialization and senile abstraction, and the inability of professors to radiate interest and enthusiasm, particularly with respect to natural history.

Don described the Chewonki semester-long course for high school students, "The Maine Coast Semester," as an attempt to practice the "lessons," teach students how to see the connections, and stimulate the sense of place that provides a necessary foundation for both lifelong learning and participation in civic life. Students take two core courses, "The Natural History of the

Maine Coast" and "Literature and the Land," along with standard courses in mathematics, history, and languages. The core courses teach ecological principles, geology, and the relations between the natural world and human culture, history, and economics, and include classroom and field exercises, discussions, and both independent and collaborative research projects. Abstract ideas are directly related to tangible experiences with local ecosystems and agriculture. Don concluded with his opinion that, for most scientists, an interest in natural history and a sense of place taught them the "big picture" first, and provided the foundation for learning about the more specialized and advanced branches of science. His concern is that this model is in danger of being lost as fewer teachers are able to convey this enthusiasm for natural history.

—LISA A. STANDLEY, Recording Secretary.

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DISTRIBUTION OF *DROSERA FILIFORMIS* AND *D. TRACYI* (DROSERACEAE): PHYTOGEOGRAPHIC IMPLICATIONS

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ABSTRACT. *Drosera filiformis* and *D. tracyi* occupy allopatric ranges, except for one restricted area in northwest Florida. *Drosera filiformis* is nearly restricted to the Atlantic Coastal Plain; *D. tracyi* is restricted to the Gulf Coastal Plain. The two species have been found to grow sympatrically in only one limited area. Natural hybrids are unknown. The distribution of *D. filiformis* is notable for its series of disjunct populations; only three other Atlantic Coastal Plain species are distributed in a similar pattern. The distribution of *D. tracyi* is continuous and without disjunctions. Many Gulf Coastal Plain species share this pattern, including close relatives of the four Atlantic disjuncts. It is postulated that the Atlantic disjuncts assumed their current discontinuous distributions through a series of short to moderately long dispersal events, followed by a loss of intervening populations. Either the Atlantic disjuncts were derived from their Gulf Coast counterparts, or both geographic groups were derived from a now extinct precursor.

Key Words: Atlantic Coastal Plain, Gulf Coastal Plain, distribution, disjunct, seepage bog, freshwater pond, Pleistocene, species pair, phytogeographic pattern

The "thread-leaved sundews" or "dew-threads" of the Atlantic and Gulf Coastal Plains have been variously treated by authors as two species, as varieties of *Drosera filiformis*, or as synonyms. *Drosera filiformis* Raf. was described early in the nineteenth century (Rafinesque 1808) and *D. tracyi* Macfarlane ex L. H. Bailey early in the twentieth (Bailey 1914). Authors who recognize them as distinct species include Clewell (1985), Godfrey and Wooten (1981), Shinners (1962), Small (1933), and Wilhelm and Burkhalter (1994). Authors opting for varietal status include Fernald (1931, 1950), Harper (1914), Kartesz (1994), Murry and Urbatsch (1979), Schnell (1976), Wood (1960), and Wynne (1944). Authors treating them as synonyms include Gleason and Cronquist (1991), Jones and Coile (1988), Lowe (1921), MacRoberts (1989), and Radford et al. (1968). Prior to Macfarlane's description of *D. tracyi* in 1914, authors used the name *D. filiformis* for plants throughout the combined range of the taxa.

I consider these two sundews to be distinct species. In the past, incomplete or inaccurate morphological descriptions and conflicting statements of range in many of the above-cited publications have obscured the distinctiveness of these species. In the Results section I present evidence to support my contention.

In this paper, the geographical ranges of *Drosera filiformis* and *D. tracyi* are examined for phytogeographic patterns, how these patterns might have evolved, and what these patterns might indicate about the origin and taxonomy of these species.

MATERIALS AND METHODS

Data on the distribution of *Drosera filiformis*, *D. tracyi*, and others discussed in this paper were obtained from direct field observations, herbarium specimens, Natural Heritage Program databases, and literature reports. Field observations were made during the past twenty-five years in nearly every state in the U.S. and the Canadian province in which these species occur. Herbarium records were obtained during visits to A, CONN, DUKE, FLAS, FSU, GA, GH, IBE, LSU, MASS, MISSA, NCSC, NEBC, NLU, NMMA, NCU, PH, USA, USCH, VDB, and VSC. Data from specimen labels are written as the collector stated. State Natural Heritage Programs have provided specimen, locality, and habitat data for critical records. Several important records came from the taxonomic and floristic literature and are cited under Distribution in the Results section.

Statistical data on species endemic to the Gulf Coastal Plain are my own, based on literature and herbarium studies.

Identification of *Drosera* specimens is based on the keys provided by Godfrey and Wooten (1981) and Shinners (1962), with corrections (see Results section). Measurements were obtained with a millimeter rule from a minimum sample of twenty-five specimens of each species.

Data on phenology and habitat were obtained from specimen labels, by direct observations of both species, and from knowledgeable botanists.

For convenience, nomenclature of taxa in this paper follows that of Kartesz (1994), except for *Drosera tracyi*, which he treats as *D. filiformis* Raf. var. *tracyi* (Macfarlane) Diels, and *Sabatia foliosa*, which he treats as *S. dodecandra* (L.) BSP. var. *foliosa* (Fern.) Wilbur.

Table 1. Comparison of selected characters of *Drosera filiformis* and *D. tracyi.*

Character	*D. filiformis*	*D. tracyi*
Leaf length	8–25 (−30) cm	30–50 cm
Scape length	6–26 cm	25–60 cm
Petal length	7–10 (−12) mm	12–17 (−20) mm
Color of glandular hairs	red to dark red	pale green
Color of dried specimen	dark red to dark brown	pale greenish brown
Color of living plant in transmitted light	reddish	white

RESULTS

Taxonomic rank of the taxa. In this section I present data that support my view that *Drosera filiformis* and *D. tracyi* are distinct species. Table 1 compares selected characters, based on herbarium specimens. These data include several corrections to keys and descriptions in the literature. For example, Small (1933) states that *D. tracyi* ranges from 3–6 cm tall, rather than 3–6 dm, apparently a typographical error. Plants of *D. filiformis* typically range from 0.8 to 2.6 dm in height. To botanists familiar with *D. filiformis* in the field, encountering a population of *D. tracyi* with leaves and scapes half a meter tall is an arresting sight. Godfrey and Wooten (1981) state that the flowering scape of *D. tracyi* has green, glandular trichomes, when in fact scapes of both species are glabrous; only the leaves bear glandular hairs. Wynne (1944) states that the petal length of *D. filiformis* is 7–15 mm and that of *D. tracyi* is 12–15 mm. Actually, petals of *D. filiformis* range from 7–10 mm (rarely to 12 mm); those of *D. tracyi* range from 12–17 mm long, with exceptionally large specimens reaching 20 mm. Petals of both species are erose along the outer margin (contra Schnell 1976). Both species may produce up to 24 flowers per raceme (contra Wynne 1944, and Godfrey and Wooten 1981), although the norm is a third to half as many (pers. obs.). With appropriate corrections in place, the keys and descriptions in Godfrey and Wooten (1981), Wynne (1944), and Schnell (1976) easily distinguish the two species.

All specimens and living plants of *Drosera filiformis* that I have seen exhibit relatively short stature, thin leaves and scapes, red glandular hairs, small flowers, and small fruits. By comparison, *D. tracyi* is robust and roughly twice as tall, with thick leaves and scapes, pale green glandular hairs, large flowers, and large fruits. An additional field character is the hue of the leaves, especially when backlit. In both species the glands produce a translucent effect, but plants of *D. filiformis* are red tinged, whereas those of *D. tracyi* are strikingly white. Photographs in Schnell (1976) show this character fairly well.

In addition to morphology, these species are phenologically and ecologically separated. Data from herbaria and my own field work indicate a blooming period from mid-April to early June for *Drosera tracyi*. *Drosera filiformis* flowers from late May to September, depending on water level (in general, onset of flowering is later with increasing latitude). Thus, there appears to be only a brief span of time in late May to early June in which the two species might hybridize. The habitat of *D. filiformis* is primarily exposed shores of freshwater ponds and lakes, but also streamside seepage bogs (New Jersey), interdune swales, coastal peat bogs (Nova Scotia), roadside depressions, and borrow pits (scrapes and depressions where sand has been extracted for road building or other uses). In contrast, *D. tracyi* occupies gently sloping seepage bogs (the term "hillside bog" is often used in the South) and ecotones between pine savannas and bay-gum-cypress wetlands. It rarely inhabits shores of sinkhole ponds (= limesinks, ponds formed in solution depressions in limestone bedrock). The bog and ecotone habitats of *D. tracyi* are maintained by recurring fires (generally 2–5 year intervals); habitats of *D. filiformis* seldom burn, except New Jersey seepage bogs and the North Carolina savannas and bays. Although the pitcher plant habitats occupied by *D. tracyi* have traditionally been called "bogs" (Folkerts 1991), they are neither peatlands nor true ombrotrophic bogs. Habitat moisture is derived primarily from acidic seepage water forced to the surface by underlying clay soils; therefore these communities are better termed oligotrophic fens or poor fens.

Finally, intermediate character states, whether in living plants or herbarium specimens, have yet to be documented. Mensural characters of the two species may overlap slightly (Table 1), but the great majority of specimens examined do not approach those values. Anderson (1991) found a site in Washington County, Florida, where the two species occurred together, with "no signs of intergradation."

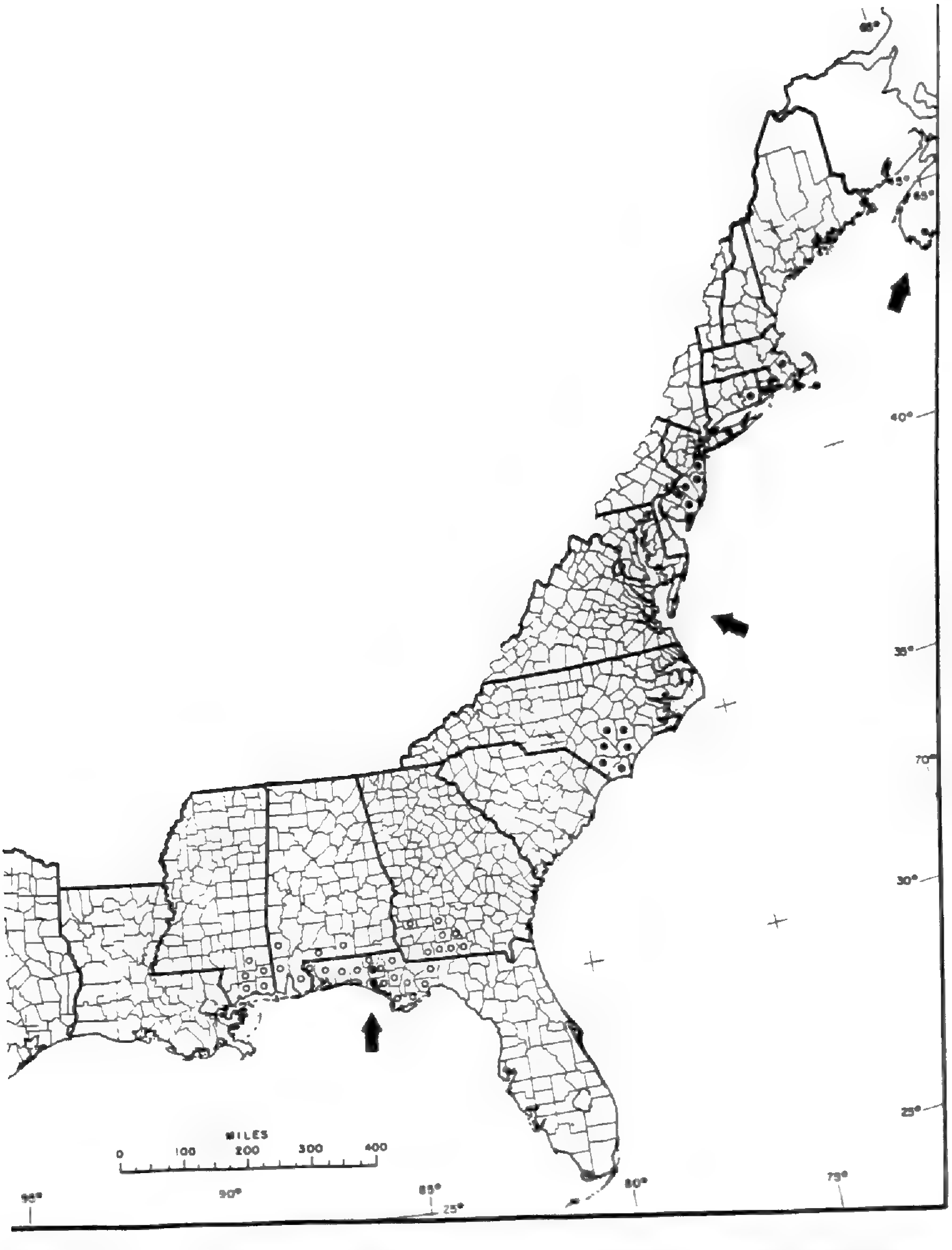

Figure 1. Distribution of *Drosera filiformis* and *D. tracyi.* Solid dots = *D. filiformis* (Nova Scotia to Florida); open circles = *D. tracyi* (Georgia to Louisiana). Note that both species occur in Bay and Washington Counties, Florida.

Distribution—*Drosera filiformis.* Figure 1 maps the distribution by county and province of *Drosera filiformis* and *D. tracyi* in the U.S. and Canada. The distribution of *D. filiformis* is composed of disjunct areas of occurrence. Except for a small area in the panhandle of Florida, *D. filiformis* occurs entirely on the Atlantic Coastal Plain.

Botanists have long known that *Drosera filiformis* occurs in the pine barrens region of Massachusetts, Long Island (New York), and New Jersey; these locations are well represented by specimens in regional and national herbaria. However, documentation of its occurrence elsewhere is poorly known, in part because these data have not been incorporated into regional manuals or monographic treatments, such as Fernald (1950), Gleason and Cronquist (1991), Shinners (1962), Wood (1960), and Wynne (1944).

In Rhode Island, a dozen *Drosera filiformis* plants were found in 1977 in a moist borrow pit near Worden's Pond in South Kingstown, Washington County (Tucker 1978). Associates included *Vaccinium macrocarpon* Aiton, *Lycopodiella inundata* (L.) Holub, and *Rhexia virginica* L.; *Tucker s.n.* (NEBC). *Drosera filiformis* was extant as of 1990, but the site is slowly succeeding to woody vegetation (R. Enser, Rhode Island Natural Heritage Program, pers. comm.). It is odd that more populations have not been found, since southern Washington County supports excellent quality pitch pine barrens, including a number of kettlehole ponds, which would seem to offer suitable habitat.

In Connecticut, *Drosera filiformis* was discovered in 1963 (Link 1965). Some 75 plants occurred in a moist borrow pit along Latimer Brook in East Lyme, New London County; *Link s.n.* (CONN). Associated species included *Vaccinium macrocarpon* Aiton, *Kalmia angustifolia* L., *Rubus hispidus* L., *Drosera intermedia* Hayne, *Iris prismatica* Pursh ex Ker-Gawler, and *Calopogon tuberosus* (L.) BSP. L. J. Mehrhoff (University of Connecticut herbarium, pers. comm.) states that this population was last seen about 1986 and that the site has become overgrown and much drier. Link (1965) also relates the discovery of a specimen of *D. filiformis* in the herbarium of the Connecticut Botanical Society from South Glastonbury, Hartford County. I have been unable to verify this record. South Glastonbury lies in a region of glacial outwash supporting coastal plain plants, and so the report is certainly plausible. It is likely that the populations in Connecticut and Rhode Island originated from propagules that invaded early successional habitats, and that these are short-lived populations. A likely source of propagules is Suffolk County, New York, where *D. filiformis* is abundant and which lies in the direction of prevailing winds.

In Delaware, Fernald (1931) mapped *Drosera filiformis* in Sussex County, but neither Tatnall (1946) nor I was able to find a voucher and the Delaware Natural Heritage Program has no verified record of its occurrence (K. Clancy, pers. comm.).

In Maryland, there are two vouchered locations. Charles County: bog adjacent to artificial lake in Cedarville State Forest, 1 Jul 1972, *Lee and Norden s.n.* (NY). This record was reported by Lee and Norden (1972). Prince Georges County: Suitland Bog, in seepage bog, introduced by A. V. Smith, growing successfully and spreading, 5 Aug 1947, *Walker 4162* (US); Suitland, open gravelly seepage, 20 Jul 1958, *Sargent 7671* (FSU). The Walker collection was reported by Shinners (1962). The earlier presence of deliberately introduced plants in an adjacent county makes the Charles County record questionable as a natural occurrence—the population could have been derived from Suitland Bog propagules. However, unless additional information indicates otherwise, the Cedarville population should be considered native.

In West Virginia, *Drosera filiformis* was reported, apparently without voucher, from Cranesville Swamp in Preston County (Breiding 1983), growing with *D. intermedia*, also a state record. These populations are considered to be introduced. Indeed, neither species has been located in several searches of the area by B. McDonald of the West Virginia Natural Heritage Program (pers. comm.).

Radford et al. (1968) documented *Drosera filiformis* from three North Carolina counties (Bladen, Columbus, and Duplin). Recent documentation exists for three additional counties. Brunswick County: disturbed pocosin along NC 211, Kologiski and McDonald, sight record (North Carolina Natural Heritage Program 1995). Pender County: open ditches along railroad, just south of Helena along SR 1412, *Sieren 3463* (WNC). Sampson County: abundant locally along grassy margins of Cutgrass Bay, with *Drosera intermedia* Hayne and *Pluchea rosea* Godfrey, 8 Jul 1989, *Sorrie 4740 with Weakley and LeBlond* (GH). Currently, there are nine extant populations in five counties (North Carolina Natural Heritage Program 1995).

In the Canadian province of Nova Scotia, a remarkable disjunct population was discovered in 1977 by J. Dowhan in an ombrotrophic, raised bog east of Barrington, Shelburne County. To my knowledge, this record has never been reported in the literature. Dowhan found an "extremely localized population in Swaine's Road Bog . . . growing in wet mud-bottom depressions . . . with *Sphagnum tenellum, S. flavicomens, Vaccinium macrocarpon, Rhynchospora alba, Sarracenia purpurea & Gymnocolea inflata*"; *Dowhan s.n.* (CONN, DAO, GH). In September of 1990 I visited a nearby bog, where numerous *Drosera filiformis* were growing with *D. intermedia* Hayne, *D. rotundifolia* L., *Ledum groenlandicum* Oeder, *Ilex glabra* (L.) Gray, *Schizaea pusilla* Pursh, and *Calamagrostis pickeringii* Gray; *Sorrie 5246* (NCU, pers. herb.). At that time, I was informed that thread-leaved sundew occurred at yet a third bog in the vicinity. All three bogs occur within two kilometers of the sea.

An even more remarkable disjunction occurs in the panhandle of Florida, discovered by R. Kral and R. K. Godfrey. There, at least eight populations are known from peaty sand shores of limesink ponds and one pond-like cypress bayhead. Dozens of other limesink ponds dot the landscape in the vicinity and more populations of *Drosera filiformis* are likely to be found. L. C. Anderson reported three collections from Washington County (Anderson 1991); otherwise, the presence of *D. filiformis* in Florida has not been documented in the literature. Bay County: sandy shores of Merial Lake north of Panama City by Florida rte. 77, 15 Jul 1970, *Kral 39938* (VDB); wet sandy shores of Merial Lake, north of Vicksburg, 10 Oct 1974, *Godfrey 73947* (FSU, VDB); exposed peaty-sandy shores of cypress head, 0.5 mi. south of jct. Florida routes 20 and 77, north of Vicksburg, 18 Sep 1982, *Godfrey 80000* (FSU); sandhills doline [= limesink or sinkhole pond] just south of Florida rte. 20, 3.7 mi. east of Crystal Lake and Florida rte. 77, 22 Jul 1991, *Kral 79463* (VDB). Washington County: limesink pond 0.7 mi. east of rte. 77, north side of Greenhead Road, 11 May 1989, *Bridges and Orzell 9785* (NCU); seepy margins of small pond in deep bowl northwest of Long Lake, south side of Greenhead Road, 2 Aug 1996, *Sorrie 8955* (GA, GH, NCU).

Wood (1960) questions the occurrence of *Drosera filiformis* in South Carolina and Georgia. I have found neither specimens nor documentation to support its occurrence there, and the state Natural Heritage Programs know of no verified record (B. Pittman and T. Patrick, pers. comm.).

Distribution—*Drosera tracyi.* In marked contrast, *Drosera* *tracyi* occurs exclusively on the Gulf Coastal Plain, from southwestern Georgia to southeastern Louisiana. The distribution of *D. tracyi* is continuous, without any disjunct populations (Figure 1).

Drosera tracyi has been well documented from Georgia, Florida, Alabama, and Mississippi, with representative specimens in regional and national herbaria. None of the Natural Heritage Programs in those states lists it as rare, except Georgia where it appears to be declining (T. Patrick, pers. comm.). Louisiana records, however, are not so well known. Riddell (1852) apparently was the first to report it from the state (as *D. filiformis*), but he gives no specific locality and there has been no voucher specimen located (MacRoberts 1989). Murry and Urbatsch (1979) cite a specimen collected in 1907, labeled "Plants of Louisiana, Wet pine barrens," *Cocks s.n.* (NO), but with no parish indicated. Fernald's generalized map (1931) shows *D. tracyi* in St. Tammany and Washington Parishes, but it is undocumented by specimens or verified sight records. On phytogeographical grounds, it is likely that Cocks secured his plants in southeastern Louisiana, for those parishes represent the western range limit for numerous species that inhabit the Gulf Coastal Plain. My own research (unpublished) on Gulf Coastal Plain endemics indicates that 160 species and varieties reach their western boundary in southeastern Louisiana.

Fernald (1950), Small (1933), and Wynne (1944) all state that *Drosera tracyi* occurs in South Carolina. Wood (1960) merely says that it has been reported from there, and Shinners (1962) likewise was unable to locate a specimen to verify the report. I, too, have failed to find any evidence of its occurrence in South Carolina. The state Natural Heritage Program knows of no verified record (B. Pittman, pers. comm.).

Drosera filiformis and *D. tracyi* occupy very distinct ranges. The former is nearly restricted to the Atlantic Coastal Plain; the latter is restricted to the Gulf Coastal Plain. Except for one limited area of sympatry in Bay and Washington Counties, Florida, the ranges of the two species are separated by a 550 km gap. In Washington County, Florida, Anderson (1991) reported finding one location where the two are actually syntopic (occurring together at a specific site).

DISCUSSION

Preparation and examination of accurate range maps can lead to the discovery of important or unusual phytogeographic patterns. By utilizing the formidable resources of the Gray Herbarium and of its library, Fernald (e.g., 1918, 1931) was able to prepare hundreds of maps that accompany his papers. These range maps were the basis for 1) establishing new regional, state, or county records, and 2) understanding the various patterns of distribution that plants exhibit. Similarly, James (1961), in his landmark paper on the endemic taxa of Florida, and Fryxell (1967), Reznicek (1994), and Wood (1972) in their papers on disjunctions, relied heavily on carefully prepared range maps. However, Fryxell stated this caution: "Yet the simple facts of distribution themselves rarely provide the basis for unequivocal interpretations. It is necessary to know . . . life form, ecological amplitude, mode of reproduction, capacity for dissemination of propagules, and cytological stability . . . before interpretations of their geographical distributions can take on solid meaning." In the previous section of this paper, I have presented data on distribution, morphology, ecology, and phenology of *Drosera filiformis* and *D. tracyi*. These data form the basis for decisions regarding taxonomic status. I believe that the data support treatment of the two as distinct species. The data also confirm the disjunct nature of the distribution of *D. filiformis* and the unbroken distribution of *D. tracyi*. In the remainder of the discussion section, I will attempt to interpret these distribution patterns in light of the historical geological context.

Forty-five years ago, Duncan (1953) questioned the availability of enough specimens to prepare adequate modern floras in the southeastern states. Perhaps as a result of this region-wide lack of distributional data, relatively few papers on the phytogeography of the Gulf and southern Atlantic Coastal Plains have been published. Since 1953, however, collections in southern herbaria have increased significantly. Floras and/or atlases are now available or are being produced in nearly every state from Virginia to Florida, Texas, and Arkansas. Gaps in our knowledge of taxonomy and distribution are rapidly becoming smaller. It seems that the time is ripe for comprehensive discussions of the phytogeography of this interesting and species-rich floristic region.

Species with similar ranges. Two other species pairs, plus a fifth species, occupy ranges that are very similar to the combined range of *Drosera filiformis* and *D. tracyi*. These species are *Coreopsis rosea* Nutt. and *C. nudata* Nutt., *Sabatia kennedyana*

Fern. and *S. foliosa* Fern., and *Lophiola aurea* Ker-Gawler. Each species pair, plus *Lophiola*, has a Gulf Coast component that is continuously distributed, and an Atlantic Coast component that has a highly disjunct distribution. Remarkably, all of the Atlantic components reach southwestern Nova Scotia, a region whose coastal plain affinities have been well documented (Roland and Smith 1969; Wisheu and Keddy 1989). Also remarkable is the fact that three of the Gulf Coast components (*C. nudata, D. tracyi*, and *L. aurea*) reach their western range limit within a few miles of each other in southeastern Louisiana. None of the seven species extends into peninsular Florida.

Sabatia kennedyana occurs disjunctly from Nova Scotia to South Carolina (Figure 2), paralleling the distribution of *Drosera filiformis*. However, *S. kennedyana* does not occur in New York, New Jersey, or Florida (Wilbur 1955). Like *D. filiformis*, it inhabits primarily sandy to boggy freshwater pond shores, where the two species often co-occur. In the Carolinas, *S. kennedyana* occurs on sandy drawdown shores of the Waccamaw River, a unique ecosystem which supports a number of "pond shore" species.

A second species of *Sabatia, S. foliosa*, occupies a more-or-less continuous distribution on the Gulf and southern Atlantic Coastal Plains (Figure 2). *Sabatia foliosa* occurs primarily in small, graminoid-shrub openings along blackwater streams (watercourses originating in the coastal plain, noted for their dark tannin-rich water), but also in pond cypress-black gum headwaters, and, in Louisiana and Texas, in marsh-like, periodically inundated depressions in pine savannas.

In the genus *Coreopsis*, two related species have distributions parallel to the two *Drosera*. *Coreopsis rosea* occurs disjunctly along the Atlantic Coastal Plain from Nova Scotia to southeastern Georgia. Over most of this range, *C. rosea* inhabits exposed shores of freshwater ponds, often in the company of *Sabatia kennedyana* and *D. filiformis*. In South Carolina, it inhabits sinkhole ponds, ponds in Carolina bays, and sandy drawdown shores of the Waccamaw River. The sole Georgia specimen (*Leavenworth s.n.*, PH) is presumably from a Carolina bay. Thus, the habitats of *C. rosea* are the same as, or analagous to, those of *D. filiformis*.

The second species of this pair, *Coreopsis nudata*, ranges from southeastern Georgia to southeastern Louisiana (Figure 3). It inhabits periodically inundated depressions which usually support

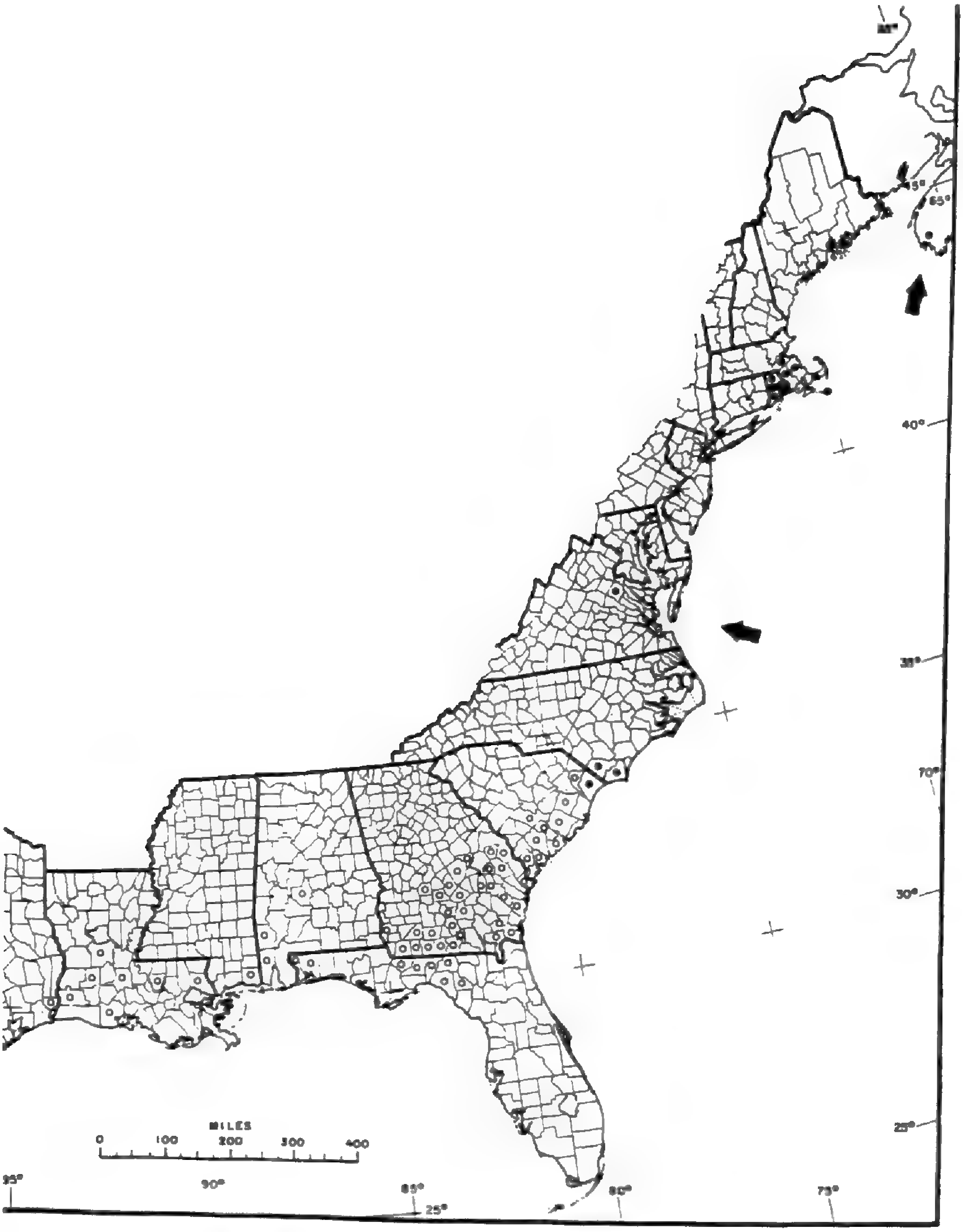

Figure 2. Distribution of *Sabatia kennedyana* and *S. foliosa*. Solid dots = *S. kennedyana* (Nova Scotia to South Carolina); open circles = *S. foliosa* (South Carolina to Texas).

pond cypress (*Taxodium ascendens* Brongn.), black gum (*Nyssa biflora* Walter), woody St. Johnsworts (*Hypericum fasciculatum* Lam., *H. chapmanii* P. Adams, and others), *Sabatia bartramii* Wilbur, and various graminoids, especially *Rhynchospora careyana* Fern. Variations of this habitat type are called cypress ponds,

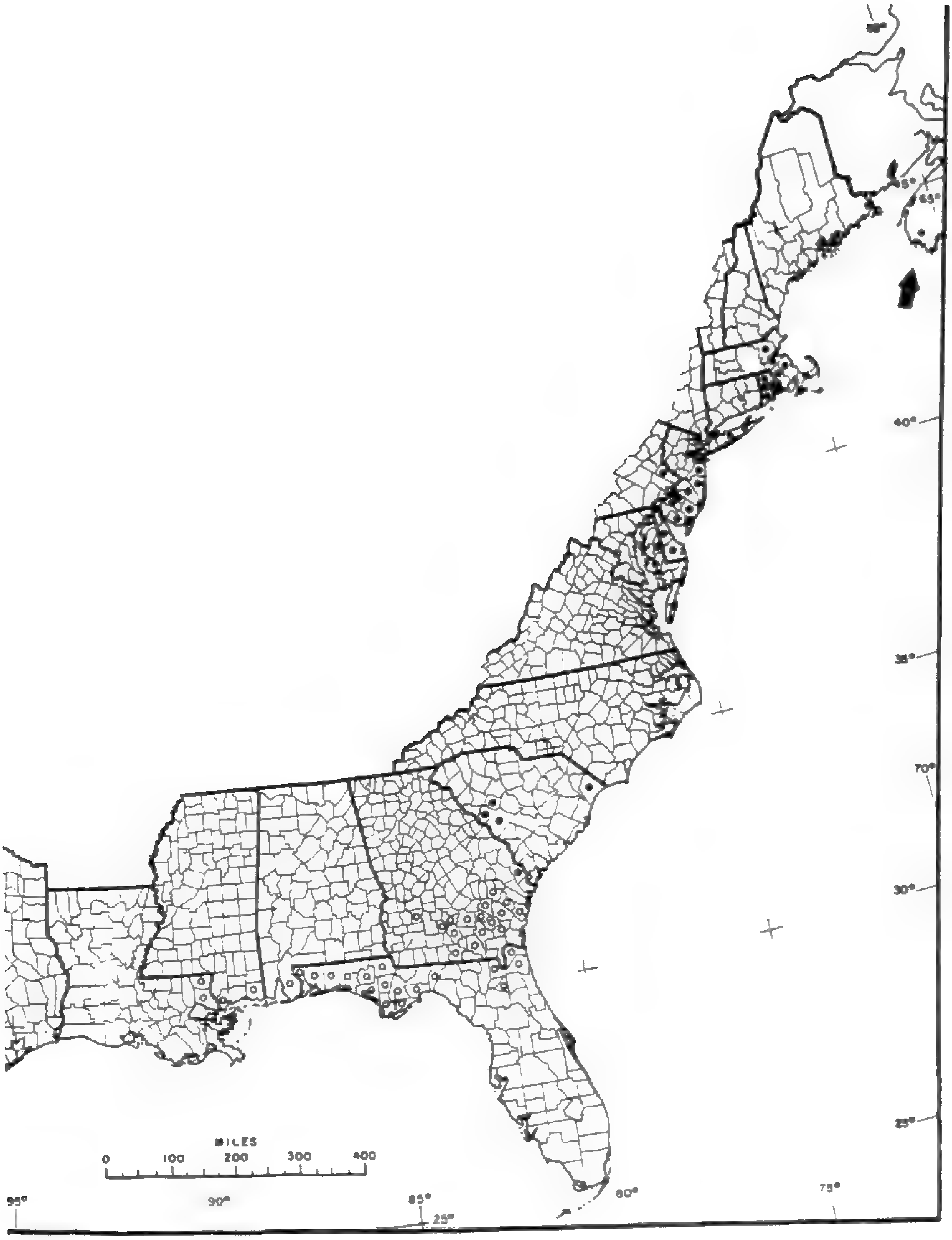

Figure 3. Distribution of *Coreopsis rosea* and *C. nudata*. Solid dots = *C. rosea* (Nova Scotia to Georgia); open circles = *C. nudata* (Georgia to Louisiana).

cypress domes, cypress stringers, and *Hypericum* ponds. Botanists often collect *C. nudata* from roadside ditches, a result of highway departments' proclivities to bisect its natural habitats. *Coreopsis nudata* does not, so far as I know, occur syntopically with *Drosera tracyi*. *Coreopsis nudata* and *C. rosea* are the only two pink-flowered species in the genus in North America, and although they are placed in the same section (Smith 1976), they possess marked differences in leaf arrangement, leaf morphology, and achene morphology. If they are to be viewed as a species pair, then it is reasonable to assume that they diverged (from a common precursor) longer ago than the split of the two *Drosera*, which have not diverged very much morphologically.

Lophiola aurea has a distribution that closely matches the combined ranges of *Drosera filiformis* and *D. tracyi.* It is primarily a Gulf Coastal Plain species, with disjunct occurrences scattered along the Atlantic Coastal Plain (Figure 4). Unlike *D. filiformis*, *Lophiola* is absent from Long Island, New York, and southeastern New England. One possible reason for this is its preference for seepage bogs and wet savannas, habitats essentially unavailable in those northern areas. In pitcher plant bogs of the Gulf Coastal Plain, *Lophiola* is abundant and is a common associate of *D. tracyi.* In North Carolina, it inhabits seasonally inundated depressions in wet, pine-wiregrass savannas and similar depressions in old river terraces. In New Jersey it occurs in streamside seepage bogs, locally called "savannas." In Nova Scotia, it occurs primarily in peaty, graminoid-dominated, riverside "savannas" (Roland and Smith 1969), but also on the shores of two lakes. Ecologically, the New Jersey and Nova Scotia "savannas" are actually acidic, poor fens, analogs of the Gulf Coastal Plain "bogs."

Fernald (1922, 1950) treated Nova Scotia plants as *Lophiola septentrionalis* Fern., but subsequent authors have not recognized them as distinct (Gleason 1952; Gleason and Cronquist 1991; Roland and Smith 1969; Scoggan 1978; Small 1933). Robertson (1976) compared Nova Scotia specimens with living plants in North Carolina and suggested that some of the variation that Fernald described may be due to ecological factors. My own observations from throughout the range lend support—rhizome thickness, corymb width, pedicel length, indument density, and capsule color (distinguishing characters used by Fernald) vary considerably. Robertson added that widely disjunct populations in a species would be expected to differ from each other. Until a detailed taxonomic study is completed, it seems best to regard *L. septentrionalis* as a synonym of *L. aurea.*

Phytogeographic patterns. The pattern displayed by the

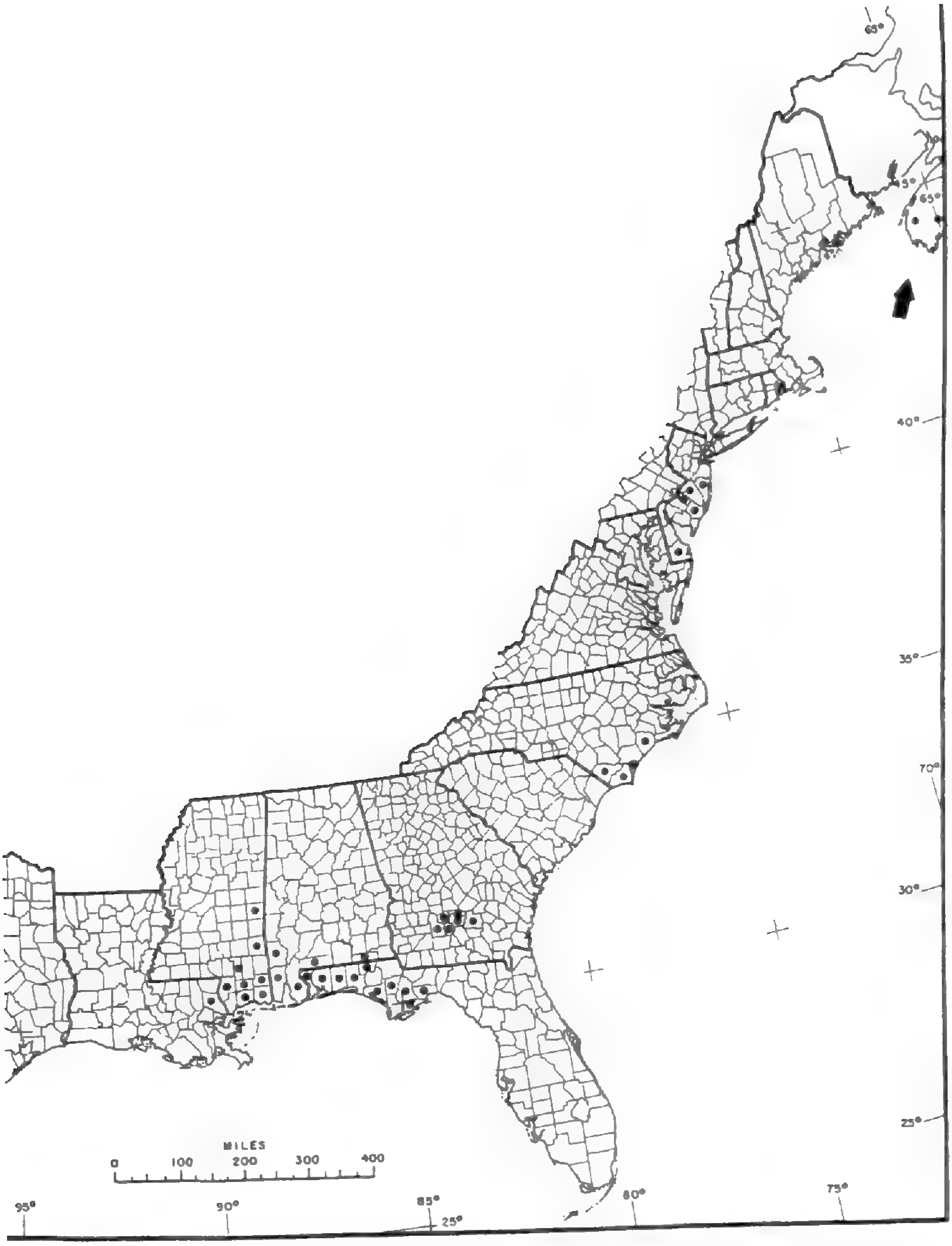

Figure 4. Distribution of *Lophiola aurea* (Nova Scotia to Louisiana).

Gulf Coast representatives of the species pairs is a common one—there are 160 taxa (species and varieties) of vascular plants which are endemic to the East Gulf Coastal Plain, a narrow band extending from southwestern Georgia through panhandle Florida to southeastern Louisiana (my own unpublished data). Another 57 taxa occupy a similar range, but extend westward across the Mississippi River to western Louisiana and/or eastern Texas. Four genera (*Brintonia* in the Asteraceae, *Harperocallis* in the Liliaceae, *Macranthera* in the Scrophulariaceae, and *Stachydeoma* in the Lamiaceae) are endemic to the East Gulf Coastal Plain, and a fifth (*Stokesia* in the Asteraceae) is nearly so. All five genera are monotypic; they may represent relicts that were more wide-ranging in the past. Clearly, Gulf Coastal Plain endemics represent a large and important component of the coastal plain flora as a whole. Ninety years ago, Harper (1907) noted that this region was a center of distribution for coastal plain plants, but no modern synthesis has been written, in part because this region remains seriously undercollected. Papers discussing phytogeographic patterns are scarce (but see Bridges and Orzell 1989a, b; Orzell and Bridges 1987).

The pattern displayed by the Atlantic Coast representatives of the species pairs is apparently unique. Many coastal plain plant taxa show minor disjunctions, but only *Coreopsis rosea*, *Drosera filiformis*, *Sabatia kennedyana*, and *Lophiola aurea* show three major disjunctions along the length of the Atlantic Coastal Plain. In the zoological realm, the distribution of the pine barrens tree frog (*Hyla andersonii*) shows two major disjunctions: from the Florida panhandle and adjacent Alabama to the Carolinas to southern New Jersey. This amphibian inhabits many of the same Gulf Coast seepage bogs as do *L. aurea* and *D. tracyi*, as well as similar bogs in New Jersey, where *D. filiformis* occurs.

I postulate that the four Atlantic disjuncts (or their progenitors) reacted very similarly to the ecological and climatic forces of the Pleistocene and that they migrated from the Gulf region out along the exposed Atlantic continental shelf as favorable conditions and habitats became available. Quaternary vegetation maps prepared by Delcourt and Delcourt (1981), based on pollen cores throughout eastern North America, suggest that the Gulf and southern Atlantic Coastal Plains supported "Oak-Hickory-Southern Pine Forest" continuously from 40,000 to 10,000 yr B. P. By 5000 yr B. P., the modern "Southern Pine Forest" had become dominant. Moreover, ". . .the Gulf Coastal Plain has remained relatively unaffected by substantial temperate changes, even during the peak in Wisconsinan continental glaciation 18,000 years ago" (Delcourt and Delcourt 1981). It seems likely that the Gulf and southern Atlantic Coastal Plains served as refugia for plants during much of the Pleistocene. Furthermore, the large numbers of endemic species (160) and genera (5) which now inhabit the East

Gulf Coastal Plain strongly suggest that the processes of speciation continued uninterruptedly during that period. In the case of *Drosera*, *Coreopsis*, *Sabatia*, and *Lophiola*, the process of migrating to the Atlantic Coastal Plain may have involved several glacial cycles, as populations became established and then extirpated. Although the taxa occupied similar habitats, each moved independently according to its dispersal capabilities. Eventually, isolation of the plant populations on the two coastal plains became great enough to allow for speciation, except in *Lophiola*.

Once populations of *Drosera*, *Coreopsis*, *Sabatia*, and *Lophiola* became established on the southern Atlantic Coastal Plain, it remained for them to move northward. Fernald (1931), Roland and Smith (1969), and others have postulated that during the last glaciation, coastal plain plants survived on the exposed continental shelf of the Atlantic Coast. The authors postulate that plants occupied continuous ranges along a broad latitudinal band. However, pollen core data (Delcourt and Delcourt 1981) suggest that during most of the past 40,000 years, the coastal plain from North Carolina northward was dominated by forests of jack pine and spruce. Under such cold climatic conditions, southern taxa were highly unlikely to survive north of the Carolinas, even in near-coastal habitats. Available evidence indicates that coastal plain plants did not occupy middle and northern Atlantic regions until after major climatic amelioration and retreat of the Wisconsin glaciers around 12,500 years ago.

Once climatic warming took place, coastal plain plants had two avenues of northward migration: incrementally by dispersing through continuous vegetation types or disjunctly via discontinuous types. Examples of species which probably migrated incrementally are *Dichanthelium scoparium* (Lam.) Gould, *Euthamia tenuifolia* (Pursh) Nutt., *Gaylussacia frondosa* (L.) Torrey & Gray, *Lyonia mariana* (L.) D. Don, and *Woodwardia virginica* (L.) Smith. These species are widespread on the coastal plain today and occupy habitats that are relatively continuous on the landscape. There is no compelling reason to doubt that such habitats were also widespread during the late Pleistocene and Holocene. Movement of propagules from one suitable habitat to another involved short-distance dispersal.

In contrast, the Atlantic species of *Coreopsis*, *Drosera*, *Lophiola*, and *Sabatia* apparently migrated disjunctly, if we assume that their habitats (ponds or poor fens) occurred discontinuously on the landscape, as they do today. As suggested by Jackson and Singer (1997) and Reznicek (1994), dispersal events may have occurred between wetlands 10–100 km apart. Although longer distances may have been successfully bridged, such dispersal events were presumably rare and are not necessary to explain the current distributions of the Atlantic disjuncts. By 10,000 yr B. P., the climate had ameliorated significantly, allowing southern plants to move northward as suitable habitats became available; about this time peat bogs developed in what is now the New Jersey Pine Barrens (Buell 1970). By 5000 yr B. P., sea level had returned to its modern position and Oak-Hickory-Southern Pine communities had reached Long Island, New York (Delcourt and Delcourt 1981). After 5000 yr B. P., there was no way for plants to reach Nova Scotia except via long-distance dispersal. Thus, plants had roughly 5000 years in which to migrate from the southern Atlantic Coastal Plain to New Jersey, southern New England, and Nova Scotia. Assuming only modest dispersal distances (less than 100 km), and allowing for local extirpations, there was ample time for plants to reach these northern areas (distance from Cape Hatteras, North Carolina, to Yarmouth, Nova Scotia is 1290 km). At the end of that period, major portions of the Atlantic Coastal Plain were inundated—Albemarle Sound, Pamlico Sound, Chesapeake Bay, Delaware Bay, Long Island Sound, Georges Bank, Bay of Fundy—and no longer available to plants. Moreover, the extirpation in those regions of coastal plain wetland plants contributed significantly to creating disjunctions on their ranges. However, it is unlikely that the extreme disjunction shown by *Coreopsis*, *Drosera*, *Lophiola*, and *Sabatia* can be explained merely by sea level rise—one of the major disjunctions occurs in the Georgia-South Carolina region, which was apparently little affected by inundation.

Dispersal of propagules from one wetland to another may happen irregularly or frequently, but successful colonization (establishment of a stable breeding population) depends on several factors. First, a species's optimal plant community may occupy only a fraction of the available wetlands, given natural variations in hydroperiod, soil nutrients, soil texture, and microclimate. Second, movement of propagules does not occur uniformly, but irregularly by mammals (including humans), waterfowl, and probably also by severe weather events. Third, successful colonization may not occur until after repeated dispersal events, as previous populations die out. Fourth, the number of wetlands decreased sharply during climatic warming as rising sea level inundated the continental shelf, especially in the mid- to north Atlantic region. As a consequence, propagules were less likely to reach suitable habitats, which in turn created disjunctions between plant populations. After the middle Holocene, northward colonization of coastal plain wetlands would have required long-distance dispersal. In my view, this is an unlikely scenario for the four species of *Coreopsis*, *Drosera*, *Lophiola*, and *Sabatia*. That all four could have such a similar pattern of disjunctions, due solely to random long-distance dispersal, is extremely unlikely. Rather, the biogeographical pattern exhibited by *C. rosea*, *D. filiformis*, *L. aurea*, and *S. kennedyana* is the product of 1) short-distance dispersal events carried out over a relatively long period of time (late Pleistocene-early Holocene); 2) different dispersal and establishment capabilities of each species; and 3) loss of intervening populations due to inundation, senescence, or other means.

The above hypothesis is speculative, but may be strengthened by additional sampling of pollen cores at sites along the length of the Atlantic Coastal Plain. Unfortunately, a critical area for such study lies in the now-inundated portion of the continental shelf. Although a considerable number of cores have been taken from the inner shelf (Emery et al. 1967; Field et al. 1979; Livingstone 1964), the relatively meager diversity of pollen recovered has not led to an increased understanding of population ecology during the Pleistocene. A major problem to overcome is the identification of pollen samples down to the species level.

In summary, available evidence suggests that populations of *Drosera*, *Sabatia*, *Coreopsis*, and *Lophiola* were neither abundant nor continuous on the continental shelf during the late Pleistocene. To account for past and present distributions, it is not necessary to assume that these taxa ranged continuously along the length of the coastal plain, nor that they migrated via long-distance dispersal events. Modern distributions of Atlantic Coastal Plain plants, including species with broad disjunctions, can be accounted for by normal dispersal and establishment during the past 15,000 years.

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ISOETES MICROVELA (ISOETACEAE), A NEW QUILLWORT FROM THE COASTAL PLAIN OF THE SOUTHEASTERN UNITED STATES

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ABSTRACT. *Isoetes microvela*, sp. nov., is described from cytologically confirmed hexaploid populations from the coastal plain of North Carolina. At least one population grows over thinly-buried calcareous bedrock, a rare condition on the predominantly acidic southeastern coastal plain. It is a large quillwort of periodically inundated and scoured stream banks and shallow water. It is characterized by a densely short-crested to reticulate-tuberculate megaspore ornamentation pattern intermediate in appearance between that of *I. appalachiana* and *I. hyemalis*, an exceptionally small velum covering ± 10% of the heavily brown-streaked sporangium, and by obscurely tuberculate microspores. A key to the *Isoetes* of the southeastern coastal plain is presented. *Isoetes microvela* is suspected to represent an allopolyploid derived from the doubling of a sterile triploid hybrid, most likely *I. ×bruntonii* (= *I. engelmannii* × *I. hyemalis*) or *I. appalachiana* × *I. engelmannii*. *Isoetes microvela* is a rare species, presently known from only two populations.

Key Words: *Isoetes microvela*, Isoetaceae, pteridophyte, coastal plain endemic, North Carolina

Twenty-four species of *Isoetes* (Isoetaceae) were identified in the *Flora of North America*, 13 of which are known from the southeastern United States (Taylor et al. 1993). A number of additional species have been recognized or described in the relatively short period since then, including *I. virginica* Pfeiffer (*s.str.*), *I. hyemalis* D. F. Brunton, and *I. appalachiana* D. F. Brunton & D. M. Britton. Sterile hybrids between a number of these taxa have recently been described (Montgomery and Taylor 1994; Musselman, Bray, and Knepper 1996, 1997; Musselman et al. 1995), confirming specific distinctions first recognized by other morphological and cytological evidence.

These taxa and the apparent existence of other undescribed species in this area (Hickey 1997) are, in part, reflections of the elevated level of interest in this genus amongst pteridologists.

They also are testaments to the taxonomic value of systematic cytological investigations of *Isoetes* populations across North America, systematic examination of *Isoetes* megaspores and microspores through Scanning Electron Microscopy (SEM), and the application of molecular and genetic investigative techniques.

Of the 16 quillwort species now known in the southeastern United States, eight are diploids ($2n = 22$), five are tetraploids ($2n = 44$), two are hexaploids ($2n = 66$), and one is decaploid ($2n = 110$). Diploid and tetraploid populations are reported for one of these, *Isoetes piedmontana* (Pfeiffer) Reed. In this paper we report the discovery of a third hexaploid taxon and offer evidence that it represents a previously undescribed endemic species of the Atlantic Coastal Plain.

MATERIALS AND METHODS

Extensive field investigations and collecting throughout the southeastern United States by Brunton since 1990 as part of ongoing systematic studies of *Isoetes* in North America have included efforts to re-locate populations of unknown or ambiguous taxa. Cytological investigations of a selection of southeastern *Isoetes* populations have been conducted by Britton during this period. Over 1500 herbarium specimens of *Isoetes* from the southeastern United States in CAN, DFB (D. F. Brunton personal herbarium), DUKE, FLAS, FSU, GA, MICH, NCSC, NCU, NYS, OAC, PH, PSU, UNA, UNCC, USF, VDB, and VPI as well as selected specimens from GH, MO, NY, and US, have been studied. Scanning electron micrographs were taken of selected samples using the standard methods of Britton and Brunton (1989, 1992).

Microspores were measured in Euparol, as described by Britton (1991). Megaspore widths (to the outer edges of spore ornamentation) were measured at a magnification of 40× or 50× on SEM stubs or in sporewells (Brunton 1990) using a binocular stereo microscope equipped with an ocular micrometer.

Chromosome counts were obtained from a selection of coastal plain *Isoetes* populations. Plants from each population were grown in distilled water in a growth cabinet. The developing root tips were excised and pretreated in aqueous paradichlorobenzene (PDB) at room temperature for four hours. They then were washed in distilled water, fixed in acetic alcohol (3:1 absolute ethyl alcohol to glacial acetic acid) for 30 minutes or more, hy-

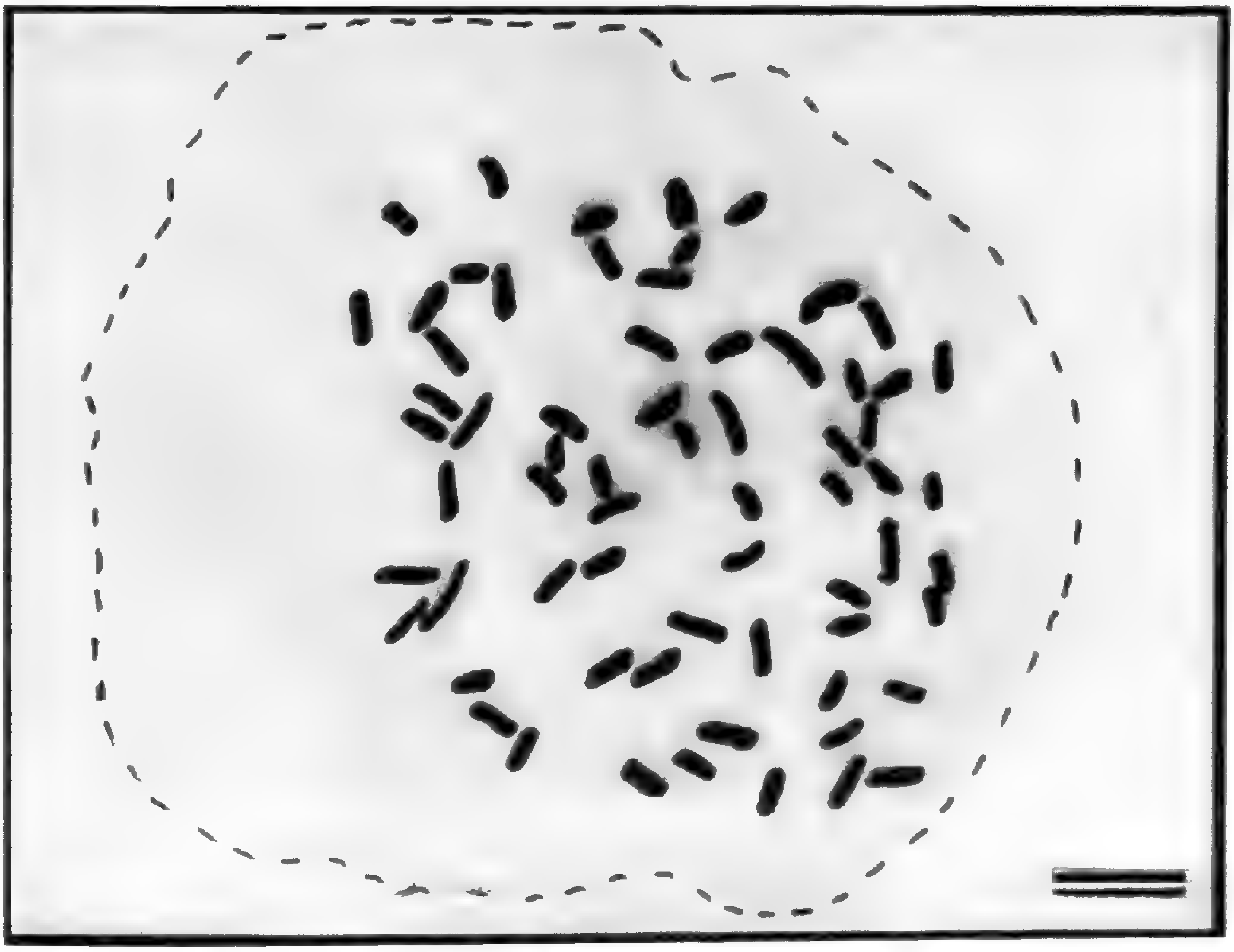

Figure 1. Interpretive drawing of photomicrograph of mitotic root tip plate of *Isoetes microvela*, $2n = 66$ (*D. F. Brunton and K. L. McIntosh 12,599* [OAC]). Scale bar = 5 µm.

drolyzed in Warmke's solution (1:1 concentrated HCl to absolute ethyl alcohol) for 7–10 minutes at room temperature, and stained in leucobasic fuchsin (Feulgen) for two hours. The meristems were squashed under a cover glass in 45% acetocarmine stain and examined.

RESULTS

An examination of herbarium specimens detected populations of large-spored *Isoetes engelmannii* A. Br. (*s.lat.*) quillworts along the coastal plain of North Carolina which could not be attributed to any existing taxon. Cytological determination of material from two North Carolina populations (Maysville, Onslow County, and Bolivia, Brunswick County; *D. F. Brunton and K. L. McIntosh 12,179* and *13,227*, respectively) indicate that they are hexaploid ($2n = 66$; Figure 1).

The two described southeastern hexaploid species, *Isoetes georgiana* Luebke and *I. boomii* Luebke, are closely related in-

Figure 2. *Isoetes microvela* plants (arrows) on emergent river bank, Maysville, Jones Co., NC (2 July 1996).

land endemics of southern and south-central Georgia (Brunton and Britton 1996a; Luebke 1992). The coastal hexaploid populations were found to exhibit consistent and distinctive morphological characteristics which readily separate them from the inland hexaploid populations. The following describes the distinctive morphological characteristics of this previously unknown coastal hexaploid.

Gross morphology. The coastal hexaploid is a large quillwort, with flaccid or strongly reflexed dark, dull olive-green leaves extending (when mature) 35 cm or more from the two-lobed corm (Figure 2). In cross-section, the leaves are ovate and are almost completely occupied by four large, thin-walled, quadrangular air chambers, the abaxial chambers being slightly larger than the adaxial. The air chambers in the leaves of the inland hexaploid species appear to be smaller, more circular, and have thicker walls. Two plants in the Maysville population were found to be joined by a short rhizome-like connection between their corms. Such a "sister" plant arrangement has previously been reported with *Isoetes hyemalis* in North Carolina (Brunton et al. 1994) and in Virginia (R. Bray, pers. comm.). In gross appearance the coastal hexaploid is not unlike many plants of the tetraploids

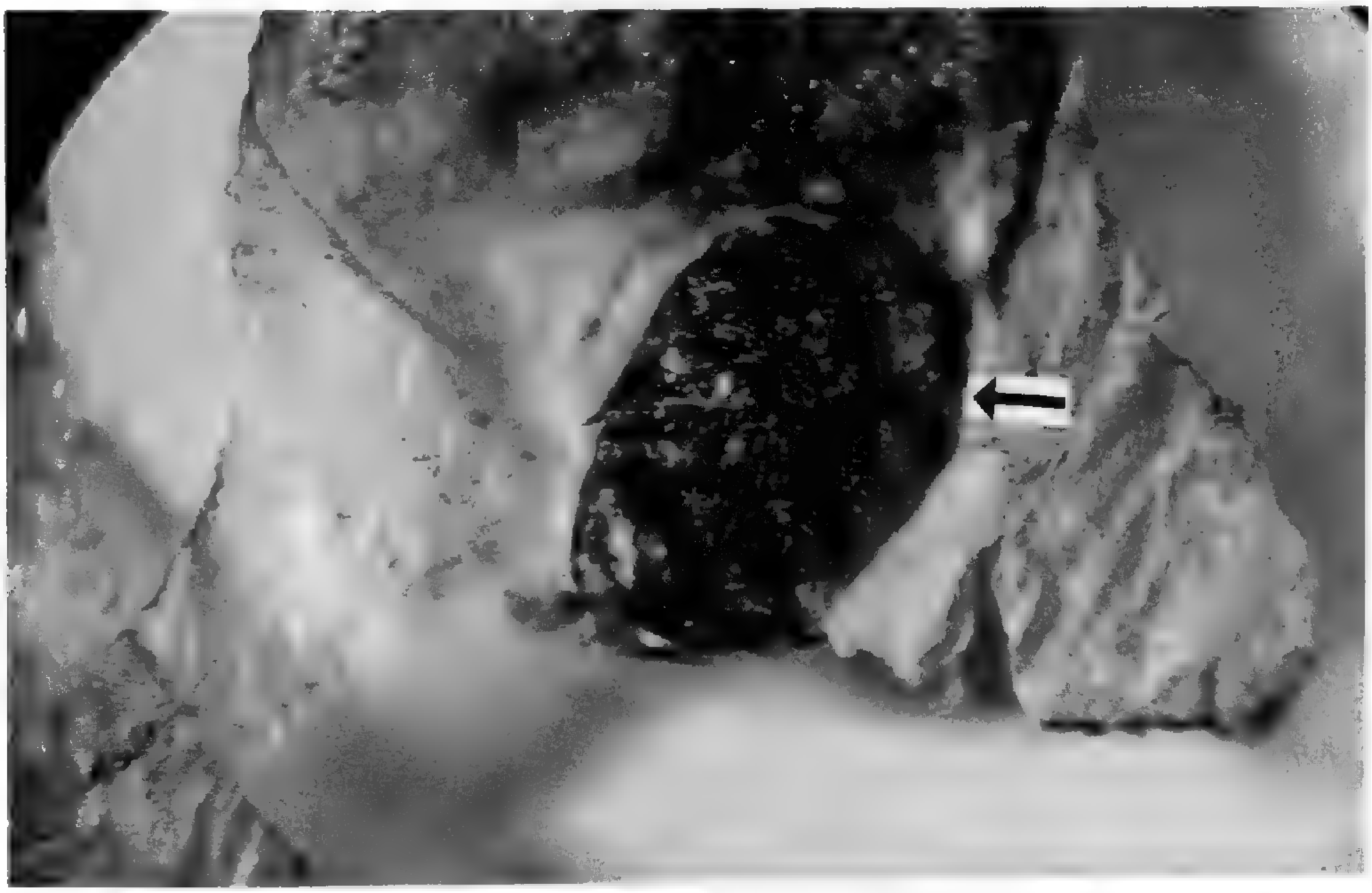

Figure 3. Sporangium of *Isoetes microvela* (*D. F. Brunton and K. L. McIntosh 13,227*); note dark sporangium (streaked) and short velum coverage (arrow).

I. hyemalis and *I. appalachiana* which we have examined from populations along the Carolina and Virginia coastal plain.

The leaf bases of this taxon are pale. Sporangia are topped by a 3.0–4.5 mm long, triangular-lanceolate ligule. The sporangium surface is heavily brown-streaked. The opaque velum is exceptionally narrow, extending across about 10% of the sporangium (Figure 3). This produces the largest fenestra (exposed "window" over the sporangium) of any of the southeastern polyploid species. It is substantially larger than the fenestra created by the 22–60% velum coverage of the Georgia hexaploids or even the 15–25% velum coverage usually observed with the tetraploids *Isoetes hyemalis* or *I. appalachiana* (Brunton and Britton 1996a, 1997; Brunton et al. 1994). Although Russell and Bray (1997) report seasonal variation in the extent of velum coverage of other southeastern hexaploids, fenestra size was consistent on the spring to summer (March to July) coastal hexaploid specimens we examined.

Megaspore size and morphology. Megaspores average ± 530 μm, although individual megaspores up to 700 μm were noted. This average is considerably smaller than that of the Georgia hexaploids (625 µm) and larger than those of the diploid *Isoetes engelmannii* (460 µm). The megaspores of the coastal hexaploid are in the size range of southeastern tetraploid species, *viz.*, *I. appalachiana* (±534 µm) and *I. hyemalis* (±522 µm; Brunton and Britton 1997; Brunton et al. 1994). The similarity of the coastal hexaploid's megaspore size to that of tetraploid taxa rather than other hexaploids is atypical of North American taxa, which normally reflect ploidy level in their spore size (Taylor et al. 1993).

The proximal (triradial) hemisphere of the megaspore is covered by a relatively dense pattern of ragged, usually thin-walled muri (walls), forming crests which join together irregularly (Figure 4e). A very narrow band of short, thin spines borders each of the proximal ridges. This proximal ornamentation pattern is substantially more congested than that of *Isoetes boomii* or *I. georgiana* (Figures 4a, 4i). Neither of the Georgia hexaploids exhibits the fine line of spines seen along the proximal ridges of the coastal hexaploid. This is, however, seen on many *I. appalachiana* megaspores.

The lateral view of the megaspore typically shows a dense, narrow band of thin spines on the distal side of the equatorial ridge (Figure 4f). This characteristic is shared with the tetraploids *Isoetes appalachiana* and *I. hyemalis*. When present, this band is composed of fewer, coarser spines in the inland Georgia hexaploids (Figures 4b, 4j; Brunton and Britton 1996a).

The distal hemisphere is dominated by a raggedly reticulate ornamentation pattern of straight-walled, evenly-topped muri (Figure 4g). As with the proximal hemisphere, this pattern is more congested than that of *Isoetes boomii* or *I. georgiana* (Figures 4c, 4k). It is similar to, but less regularly reticulate than, the distal megaspore ornamentation of *I. appalachiana*. The megaspore ornamentation of the coastal hexaploid usually includes isolated and/or loosely connected tubercles reminiscent of the megaspores of *I. hyemalis*. The overall ornamentation pattern, then, appears intermediate between that of *I. appalachiana* and *I. hyemalis* and is considerably more congested than that of the other hexaploids of the southeastern United States.

Microspore size and morphology. Microspores of the coastal hexaploid are ±29 µm long. This is substantially smaller than the Georgia hexaploids (±37 µm) and approximately equal to

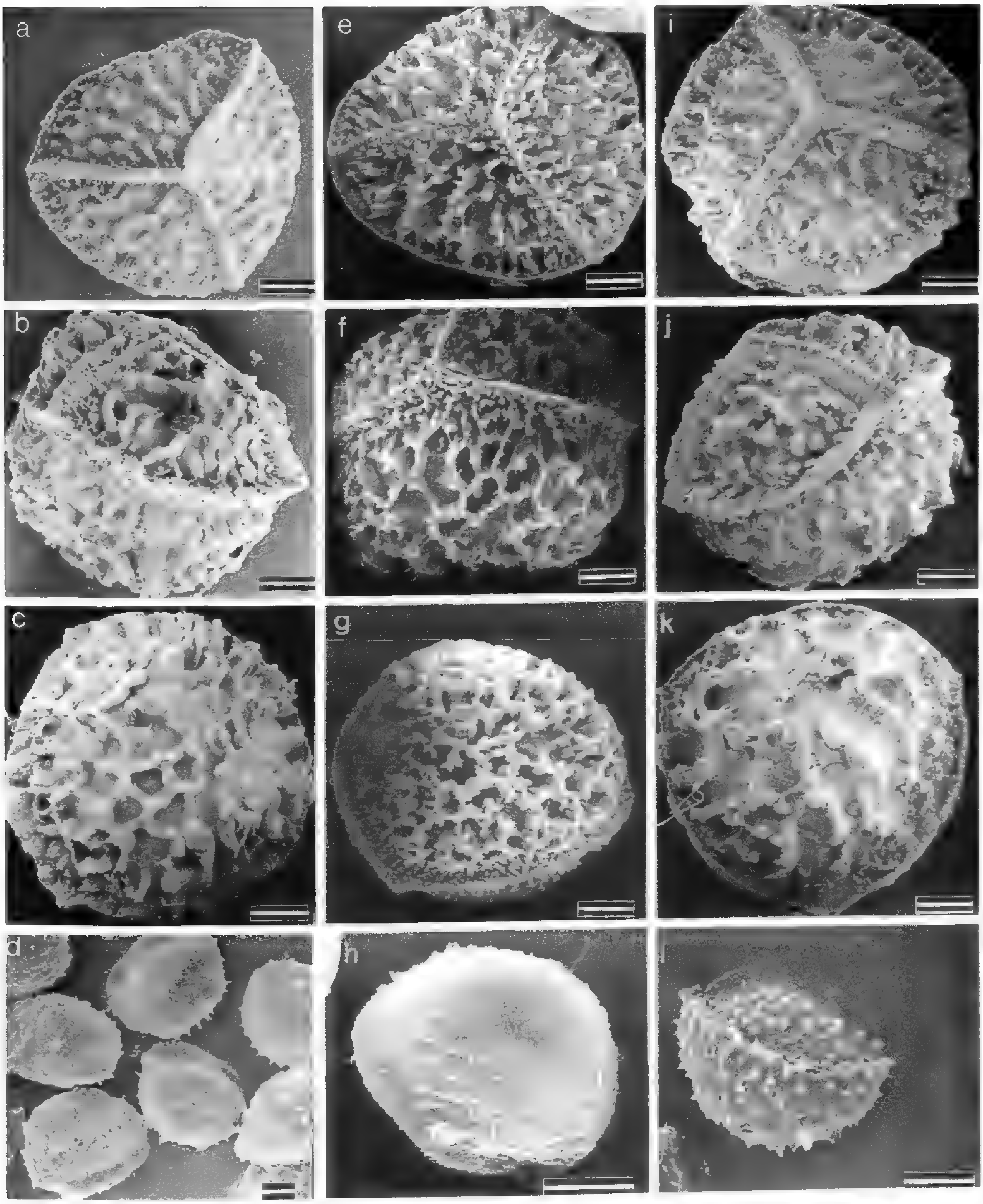

Figure 4. Spores of southeastern hexaploids *Isoetes boomii*, *I. microvela*, and *I. georgiana* (megaspore scale-bar = 100 μm; microspore scale-bar = 10 μm). a–d: *I. boomii* (*D. F. Brunton and K. L. McIntosh 12,063* [OAC]): a: proximal view of megaspore; b: lateral view of megaspore; c: distal view of megaspore; d: group of microspores; e–h: *I. microvela* (megaspores, *D. F. Brunton and K. L. McIntosh 12,213* [OAC]; microspore, *A. E. Radford 5,187* [NCU]); e: proximal view of megaspore; f: lateral view of megaspore; g: distal view of megaspore; h: microspore; i–l: *I. georgiana* (*D. F. Brunton and K. L. McIntosh 11,550* [OAC]); i: proximal view of megaspore; j: lateral view of megaspore; k: distal view of megaspore; l: microspore.

that of tetraploids such as *Isoetes appalachiana* (±30 μm; Brunton and Britton 1996a, 1997). Surface ornamentation is lacking or consists of small, low, sparsely distributed tubercles (Figure 4h). The Georgia hexaploids, in contrast, are aculeate (covered in short, broad-based prickles; Figures 4d, 4l). The microspores of both *I. appalachiana* and *I. hyemalis* are low tuberculate to echinate (Brunton and Britton 1997; Brunton et al. 1994).

Microspores were rarely observed on plants from either cytologically confirmed population; only one plant with mature microspores has been found in collections from each of the Maysville and Bolivia populations. We have found microsporophylls to be substantially more common on all other southeastern species. Finding virtually entirely microsporangiate populations, in fact, can be an impediment to the identification of some *Isoetes* populations in the southeast.

Site ecology. The coastal hexaploid occupies habitats strongly affected by storm-induced flooding. Both cytologically confirmed populations were found along permanent water courses under the deep shade of deciduous swamp forests. The plants grow in sandy alluvium, usually with little or no associated vascular vegetation in shallow water or (more commonly) on seasonally exposed stream or river banks. At the Maysville site at least, the thinly-buried bedrock is calcareous (sedimentary shellstone); this is a rare occurrence in a region of predominantly heavily weathered, acidic soils (LeBlond et al. 1994; Steila 1993).

The Maysville site was severely scoured by post-hurricane flood waters and waterborne debris in late 1996 and early 1997. This erosion resulted in the loss of a substantial proportion of the thin soil covering from the shellstone bedrock and caused the apparent destruction of many *Isoetes* plants (D. F. Brunton, pers. obs.).

Distribution and status. Two cytologically confirmed populations are found along the North Carolina coast. A small population occurs at Bolivia, Brunswick County. A larger population near Maysville extends along either side of the Jones/Onslow County border (Figure 5). In addition, Musselman, Bray, Heafner, and Knepper (1997) report a hexaploid from Florida which may represent this taxon.

Considering the few known sites and the low number of can-

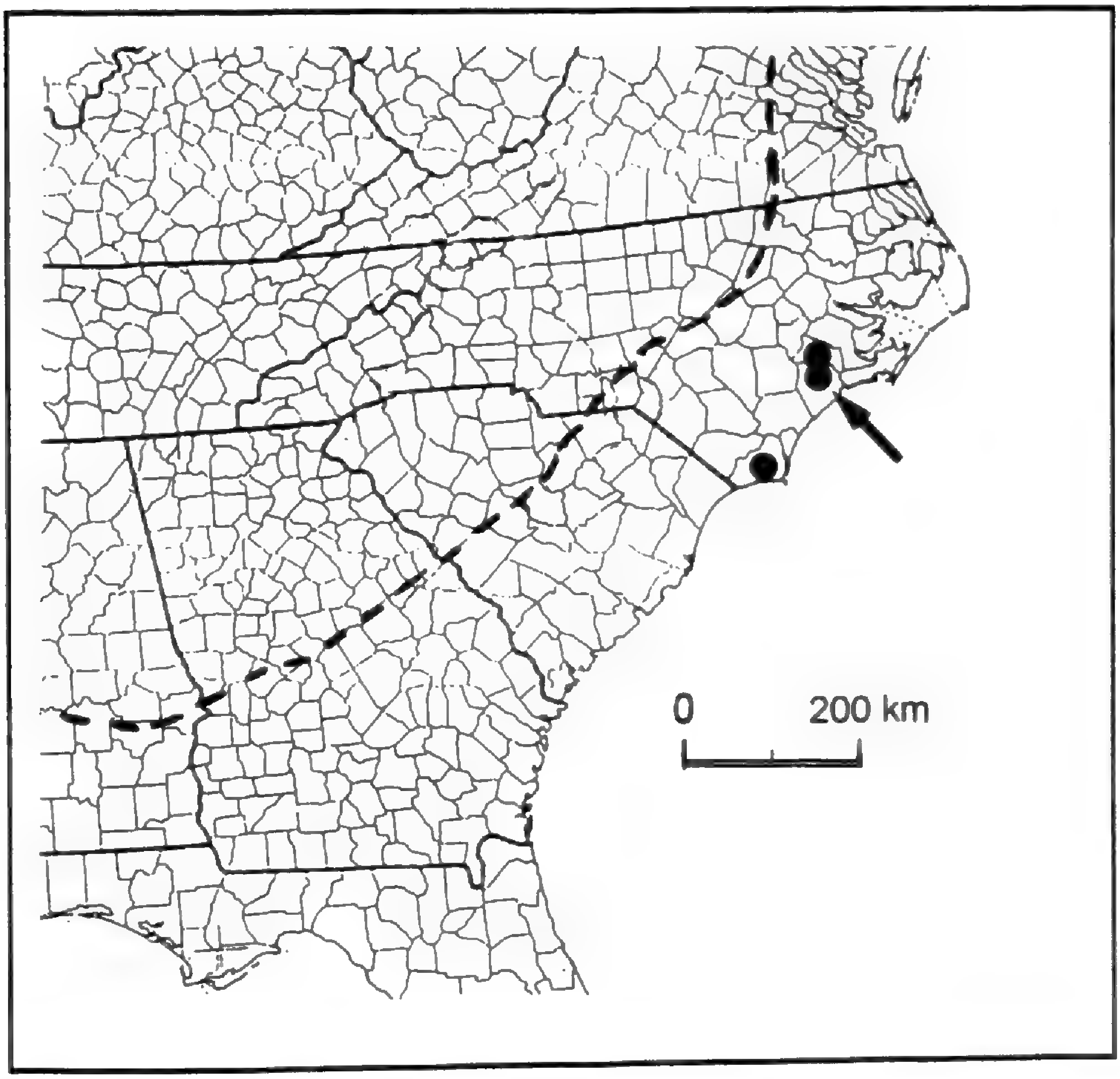

Figure 5. Distribution of *Isoetes microvela* in the southeastern United States (dotted line = boundary between coastal plain and Piedmont; arrow = Type location).

didate populations, this hexaploid appears to represent a legitimately rare Atlantic Coastal Plain endemic of the southeastern United States. A number of similarly rare endemic vascular plants are also known from this area, including the recently described *Carex lutea* LeBlond and *Thalictrum cooleyi* Ahles. The latter two species are found in sandy soil over calcareous bedrock, a rare substrate condition in the southeastern coastal plain (LeBlond et al. 1994) that is also shared by the Maysville population.

DISCUSSION

The characteristics of the coastal plain hexaploid populations indicate they constitute a distinct, small-spored hexaploid species. This new taxon has a megaspore ornamentation intermediate between that of the tetraploids *Isoetes hyemalis* and *I. appalachiana*, an exceptionally short velum, and plain to obscurely ornamented (and rarely observed) microspores. Accordingly, the following binomial is proposed.

Isoetes microvela D. F. Brunton, *sp. nov.* (Figures 1, 2, 3, and 4e–h). TYPE: U.S.A. North Carolina: Onslow Co., Maysville, banks of White Oak River, 21 May 1995, *D. F. Brunton and K. L. McIntosh 12,179* (HOLOTYPE: OAC; ISOTYPES: MIL, US, MICH, MU, DAO, DFB, ODU).

Herba amphibia e cormo bilobo; folia angusta (<2 mm), perviridia, flaccida vel reflexa usque ad 40 cm longa; velum opacum, tegens plus minusve supremam decimam partem sporangii copiose brunneostriati; megasporae ±530 μm, obtectae latere distali ab ordinatione cristarum humilium et irregularium atque tuberculorum gracilium dense reticulata, latere proximali ab ordinatione iugorum et tuberculorum irregulari, et habentes zonam spinarum breviorum in latere iugi aequatorii distali; microsporae ±30 mm, vel parum obscure tuberculatae vel inornatae; chromosomata $2n = 66$.

FORM: Amphibious perennial herb arising from a 2-lobed corm, solitary or occasionally two joined at the corm; LEAVES: 20–25 (occasionally to 50), narrow (1.1–1.7 mm wide at midpoint), dark green when mature, 35–40 cm long, strongly reflexed or flaccid, flattened-oval in cross-section and occupied largely by four thin-walled air chambers (abaxial chambers slightly larger) and a central vascular bundle, becoming paler with narrow hyaline margins at the base; LIGULE: lanceolate-triangular, delicate, 3.0–4.5 mm long; VELUM: opaque, covering 9.45% (SD 1.56, N = 28) of the sporangium; SPORANGIA: ovate, ±6 × 4 mm, embedded into the basal adaxial side of the sporophylls; densely marked with light brown to dark brown streaks; MEGASPORES: white, 526.9 μm (SD 27.1, N = 79); with dense reticulate ornamentation pattern of irregular crests and thin tubercles on the distal side; irregularly radiating pattern of ridges and tubercles on the proximal hemisphere; short spines evident along the proximal ridges; dense band of short spines borders distal side of the equatorial ridge; spores are mature May–July (September ?); MICROSPORES: 29.8 μm (SD 2.28, N = 20), oval, plain or ornamented with small, low, sparsely distributed tubercles; CYTOLOGY: $2n = 66$. The epithet reflects the consistently short velum found over the sporangia of this species, significantly shorter than that of all other polyploids in the southeastern United States.

PARATYPES: NORTH CAROLINA: Brunswick Co., Bolivia, Bolivia Branch of Middle Swamp, *A. E. Radford 5,187*, 2 Jun 1950 (NCU); *D. F. Brunton and K. L. McIntosh 12,599*, 3 Jul 1996 (OAC, DFB); *D. F. Brunton and K. L. McIntosh 13,227*, 29 Jun 1997 (OAC, DFB); Jones Co., Maysville, E bank of White Oak River, *D. F. Brunton and K. L. McIntosh 12,579*, 2 Jul 1996 (OAC, DFB); Onslow Co., Maysville, banks of White Oak River, *D. F. Brunton and K. L. McIntosh 12,213*, 23 Jun 1995 (OAC, DFB).

The following key to the species of *Isoetes* found along the southeastern coastal plain will assist in the discrimination of *I. microvela* from morphologically similar quillworts in that area. The megaspore figures represent the approximate average size from the specimens we examined and are provided as general guidelines. Discussions of more precise calculations of megaspore and microspore size variation can be found in recent literature concerning southeastern species, including Brunton and Britton (1996a, b, 1997), Brunton et al. (1994), Russell and Bray (1997) and Taylor et al. (1993). Size and morphological exceptions and extremes can be encountered with most of these taxa. Accordingly, *I. microvela* is keyed through each of the two main size and megaspore pattern options.

1. Megaspores >600 µm .... (2)
    2. Megaspore ornamentation ±thin-walled; velum ±10% .... *I. microvela*
    2. Megaspore ornamentation thick-walled; velum ≥30% .... (3)
        3. Megaspore ornamentation coarse; ridges with thick walls in open pattern; velum ±60% .... *I. georgiana*
        3. Megaspore ornamentation somewhat coarse; ridges with moderately thick walls in ±congested pattern; velum ±30% .... *I. boomii*
1. Megaspores <550 µm .... (4)
    4. Velum covering >50% of sporangium .... (5)
        5. Leaves yellow-green, weakly erect to reflexed, 15–40 cm long; velum covering 50–70% of the unmarked sporangium; megaspore ornamentation

high-walled, with ragged-reticulate pattern .... *I. valida* (Engelm.) Clute

5. Leaves dark green, flaccid, 25–60 cm long; velum covering 80–100% of unmarked or sparsely brown-streaked sporangium; megaspore ornamentation of low, broad tubercles or ridges ... . *I. flaccida* Shuttlew.

4. Velum covering <50% of sporangium .... (6)
    6. Megaspores reticulate (evenly or irregularly) ... (7)
        7. Megaspores ±450 μm; evenly reticulate ornamentation with ±thin walls; no equatorial band of spines ..... *I. engelmannii* (*s.str.*)
        7. Megaspores >525 μm; unevenly reticulate ornamentation with ±thick walls; obscure to distinct equatorial band of low, thin spines .... (8)
            8. Velum 20–25%; megaspores with ±open, irregularly reticulate pattern; microspores with low tuberculate ornamentation .... *I. appalachiana*
            8. Velum ±10%; megaspores with ±congested, densely reticulate ornamentation pattern; microspores plain or sparsely ornamented with low tubercules ... . *I. microvela*
    6. Megaspores tuberculate to irregularly and densely short-crested .... (9)
        9. Leaves 10–20 cm long; velum 25–30%; megaspore with moderately low, densely short-crested to tuberculate ornamentation; distinct equatorial band of short spines; outer shell (perispore) ±crumbly-surfaced; microspores with few, low, echinate tubercles .. .. *I. riparia* Engelm. ["*saccharata*"]
        9. Leaves 20–45 cm long; velum <25%; megaspore with ±high, tuberculate to short-crested ornamentation; obscure to distinct equatorial band of short spines; perispore ± smooth-surfaced; microspores obscurely low tuberculate to conspicuously echinate .... (10)

10. Megaspore ornamentation of tubercles and short crests; velum 15–20%; microspores densely echinate. . . *I. hyemalis*
10. Megaspore ornamentation short-crested to irregularly reticulate with few tubercles; velum 10%; microspores with obscurely tuberculate ornamentation . . . . *I. microvela*

Origins. Most, if not all, North American polyploid *Isoetes* are believed to represent allopolyploids, as has been demonstrated for *I. riparia* (Taylor and Hoot 1997; Taylor et al. 1985) and *I. appalachiana* (W. C. Taylor, pers. comm). The hexaploid *I. microvela* could represent the allopolyploid product of the chromosome doubling of a sterile hybrid between a diploid and a tetraploid (*viz.*, $2x \times 4x = 3x$ [doubled] $= 6x$). Assuming that the resulting species would tend to reflect the morphological characteristics of both progenitor species, a number of *Isoetes* taxa occurring in the southeastern United States can be considered as candidate ancestors for *I. microvela*. These include diploids *I. engelmannii*, *I. flaccida*, and *I. valida*, and tetraploids *I. appalachiana* and *I. hyemalis*. Of the diploids, *I. valida* and *I. flaccida* seem unlikely to be involved since evidence of their large velum (50% or more) and densely echinate microspores (Brunton and Britton 1996b; Taylor et al. 1993) are not seen in *I. microvela*. If *I. engelmannii*, then, is the most likely diploid progenitor, we are left to determine whether *I. appalachiana* or *I. hyemalis* is the most probable tetraploid parent.

Were *Isoetes appalachiana* the tetraploid parent, one might expect an *I. microvela* megaspore pattern that is more evenly reticulate and which does not include tubercles. Although we did not employ ligule characteristics when considering possible progenitor species because of our limited understanding of this delicate structure, *I. hyemalis* appears to be the only other existing southeastern taxon with as large a ligule as *I. microvela* (J. Hickey, pers. comm.). The participation of *I. hyemalis* is also suggested by the occurrence of occasional *I. microvela* "sister" plants joined at their corms, a characteristic known otherwise amongst North American polyploids only with *I. hyemalis*. An origin involving *I. hyemalis* as the tetraploid progenitor, however, may not be well supported by the obscure microspore ornamentation of *I. microvela.*

The combination of megaspore and leaf characteristics of *Isoetes microvela* described above is close to that of *I. ×bruntonii* Knepper & Musselman, the sterile triploid hybrid *I. engelmannii* × *I. hyemalis* (Musselman et al. 1996). On the basis of morphological evidence, therefore, *I. microvela* appears to represent an allopolyploid of *I. ×bruntonii* or possibly *I. appalachiana* × *I. engelmannii.*

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ADDENDUM. After the manuscript was in proof an additional population of *Isoetes microvela* was discovered along River Swamp, a tributary of Lockwood Folly River, 6.0 km south of Bolivia, Brunswick County, NC. Although severely wilted by prolonged exposure, scattered plants were observed growing with bryophytes (liverwort) and occasional graminoid seedlings through a dense mat of tree rootlets in fine sand on a creek bank 0.5-1.0 m above the present water level in a seasonally flooded swamp forest. A collection from this population (*D.F. Brunton and K.L. McIntosh 13,601*, 11 Jul 1998, OAC) was cytologically confirmed $2n = 66$.

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ALLOZYME DIVERSITY IN *AMELANCHIER ARBOREA* AND *A. LAEVIS* (ROSACEAE)

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ABSTRACT. We examined allozyme variation in five populations of *Amelanchier laevis*, which is known to be a facultative apomict in Maine, and four populations of a closely allied species, *A. arborea*. While *A. laevis* had slightly less genetic variation than *A. arborea* and less than half the number of multilocus genotypes per population, ranges of these parameters overlap extensively for the two species. Therefore, overall, these two species are comparable in the amount and distribution of their allozyme variation. Both species also had less diversity than expected based on their life history traits. Little interpopulation genetic differentiation occurred in either species, perhaps due to gene flow via avian fruit dispersal. Genetic identities are quite high among populations within each species as well as between the two species. In fact, each *A. arborea* population was more similar to at least one *A. laevis* population than to other *A. arborea* populations. *Amelanchier laevis* populations were also more similar to populations of the other species except in the case of two of the Maine populations. Recent morphological diversification and/or extensive hybridization in the genus may account for these results. Studies of additional *Amelanchier* species would indicate whether or not the level and pattern of genetic variation and the high genetic similarities of these two taxa are representative of the genus.

Key Words: *Amelanchier*, apomixis, allozymes, genetic diversity, Maloideae, Rosaceae

Among asexual woody plants, studies of allozyme variation in natural populations have focused almost exclusively on vegetatively reproducing plants (e.g., Barnes 1966, 1969; Comtois et al. 1986, 1989; Hermanutz et al. 1989; Jelinski and Cheliak 1992; Sherman-Broyles et al. 1992). Species in many angiosperm families, however, produce seeds asexually by a process called apomixis or agamospermy (Asker and Jerling 1992; Richards 1986). Yet, although several widespread woody genera have predomi-

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nantly apomictic species (e.g., *Amelanchier, Citrus, Crataegus, Euonymus, Malus, Mangifera,* and *Sorbus*; Richards 1986), few studies of genetic diversity in such species exist.

The maloid genera of the Rosaceae are characterized by extensive hybridization, polyploidy, and apomixis (Campbell et al. 1991; Dickinson and Campbell 1991; Phipps et al. 1991). Based on traditional views apomixis should lower genetic diversity within populations (reviewed in Asker and Jerling 1992; but see Marshall and Weir 1979 and Overath and Asmussen 1998 for a contrary view), while hybridization and polyploidy are usually associated with higher levels of genetic diversity (Moody et al. 1993). In contrast, Hamrick et al. (1992) found that woody species capable of both sexual and asexual (mainly vegetative) reproduction have as much or more allozyme diversity as sexually reproducing species. Since apomicts that have been studied in detail are capable of at least some sexual reproduction (Asker and Jerling 1992), such facultative apomicts may also fit this pattern. However, the fact that apomicts can clonally disperse long distances (via seeds) while vegetative dispersal is local (via stolons, runners, etc.) complicates the picture.

At least six maloid genera contain apomictic species (Asker and Jerling 1992; Campbell et al. 1991). In studies of morphological variation in maloid species, Campbell and Dickinson (1990) found that morphological variation in *Amelanchier, Crataegus,* and *Sorbus* was associated with the breeding system; apomictic species had somewhat less variation than sexual species. Although this difference was significant in their first study, it was appreciably less so when more populations were included (Dickinson and Campbell 1991). A more recent study of the amounts and distribution of morphological variation in *Amelanchier* revealed significantly more variation in the sexual species but no difference in how genetic variation was apportioned among populations (Campbell et al. 1997).

Studies of allozyme diversity in maloid species have yielded variable results. Proctor et al. (1989) found dramatic differences in a study of peroxidase diversity among *Sorbus* species in England: populations of polyploid apomicts contained almost no variation, while in diploid sexual populations genetically unique individuals could be recognized. In contrast, Aas et al. (1994) found morphological and isozyme variation, as well as evidence for sexual reproduction, in German populations of *S. latifolia,* one of the apomictic species in the English study (Proctor et al. 1989). In a study of allozyme diversity in natural populations of several North American *Malus* species, Dickson et al. (1991) found slightly less genetic diversity than the average for long-lived woody species (Hamrick and Godt 1989). One of the species studied, *M. coronaria*, is considered an apomict (Campbell et al. 1991).

Due to apomixis, polyploidy, and hybridization the woody genus *Amelanchier* Medikus is taxonomically confusing and, thus, has been the subject of much morphological study (e.g., Campbell and Dickinson 1990; Campbell et al. 1997; Cruise 1964; Dickinson and Campbell 1991; Wiegand 1912). Campbell, with various coworkers (Campbell et al. 1985, 1987; Weber and Campbell 1989), documented facultative apomixis in several taxa in this genus. We chose to study two closely allied *Amelanchier* species, which we initially presumed to differ in reproductive mode (sexuality), *A. laevis* Wieg. and *A. arborea* (Michx. f.) Fern.

Both species are shrubs or small trees and widespread in eastern North America. Their distributions are similar and largely overlapping. *Amelanchier laevis* ranges from southern Canada to northern Georgia, while *A. arborea* ranges as far south as Florida (Gleason and Cronquist 1991). These species are similar enough morphologically that some have suggested lumping them into a single species (e.g., Cruise 1964). The main morphological differences appear to be (1) young leaves are hairy on the lower surface early in the season in *A. arborea* and glabrous in *A. laevis*, (2) leaves at anthesis are less than half-grown in *A. arborea* and half-grown in *A. laevis*, and (3) fruits are red-purple and dry in *A. arborea* and dark purple and juicy in *A. laevis* (Fernald 1950; Gleason and Cronquist 1991).

Campbell et al. (1985) documented apomixis in a Maine population of *Amelanchier laevis*, while Gorchov (1988) described *A. arborea* as sexual in Michigan. However, because these species have been described as both tetraploids (Campbell et al. 1985; Cruise 1964) and diploids (Robinson and Partanen 1980) and since most polyploid Maloideae are capable of apomixis (Campbell et al. 1991), the breeding system may differ among populations of both species. Moreover, Campbell et al. (1987) suggested that ploidy level may be associated with latitude in this genus because diploid chromosome counts come from the southern part of the northeastern United States (e.g., New Jersey). If so, reproductive mode may also vary with latitude.

Few woody apomicts and maloid species have been studied using genetic markers such as allozymes. Our study addresses this situation by describing patterns of allozyme variation within and among populations of *Amelanchier laevis* and *A. arborea*. In addition to comparing levels and patterns of genetic variation between these two species, we examined the data for geographic patterns in the levels of genetic diversity that may be indicative of differences in ploidy level or sexuality. Finally, since allozymes have proven useful in evaluating species delineations in other maloids (e.g., *Malus*; Dickson et al. 1991), our results may also provide preliminary information concerning Cruise's (1964) proposal to combine these two taxa.

MATERIALS AND METHODS

We collected leaves and twigs from five populations of *Amelanchier laevis* and four populations of *A. arborea* from Maine to Georgia (Figure 1). For each collecting site, we contacted local experts to determine which species were present and, when possible, had their assistance in collecting the appropriate species. Given the taxonomic uncertainty associated with this genus, some genetic diversity may represent undetected taxonomic diversity in our samples. In addition, cryptic hybridization has been implicated as a source of morphological variation within *A. laevis* (Campbell et al. 1997). (Unfortunately, voucher specimens were inadvertently destroyed.) Population 3L contains some *A. canadensis* individuals, which were not included in this study, and populations 6L and 7A are actually from one area (forest around Mountain Lake Biological Laboratory) that contained both species, although generally not intermixed; the other sites appeared to contain only one species. All adult individuals of the target species were sampled in each population (except those with more than 48 individuals in which case only 48 individuals were sampled). Samples were kept on ice until returned to the laboratory where they were frozen in liquid nitrogen and ground with a mortar and pestle. Proteins were extracted from leaves with a phosphate polyvinylpyrrolidone buffer (Mitton et al. 1977). The leaf extract was absorbed onto Whatman #3 chromatography paper wicks and stored at −70°C until analysis. Using horizontal

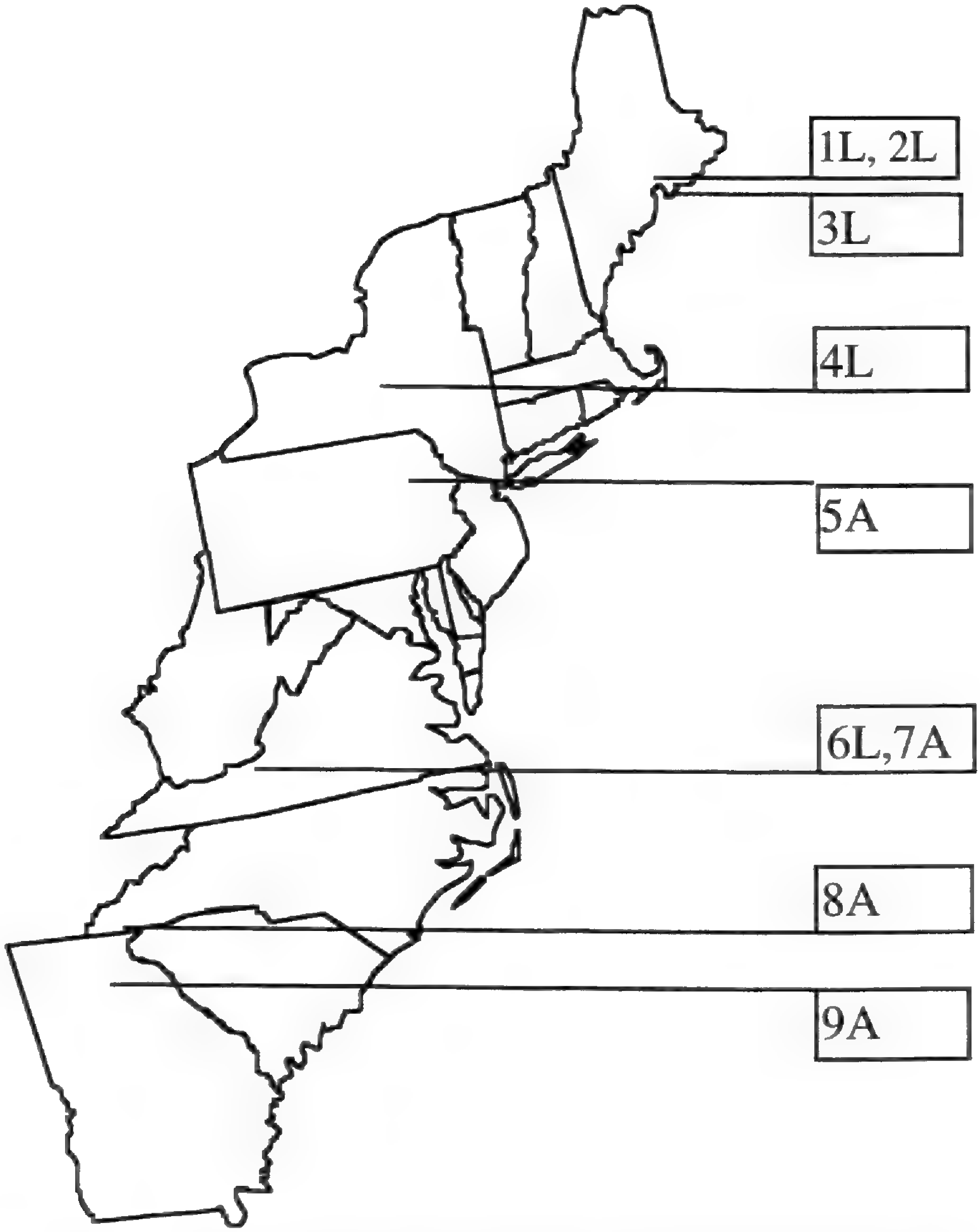

Figure 1. Locations of the nine *Amelanchier* populations sampled. Letters after the numbers refer to the species: L = *A. laevis*, A = *A. arborea*. The populations are: 1L = between two fields on Burleigh Rd., Bangor, ME; 2L = roadside on Stillwater Ave., Bangor, ME; 3L = open field on Rt. 175, near Sedgewick, ME; 4L = along trail at Hoxie Gorge, near Cortland, NY; 5A = in Schoch Heath, west of Schoch Mill Road north of Schoch Creek, in township of Penn Forest, PA; 6L and 7A = understory in forest around Mountain Lake Biological Laboratory, Mountain Lake, VA; 8A = along the Yellow Mountain Trail, Highlands Ranger District, Nantahala National Forest, near Highlands, NC; 9A = near trails in Thompson Mills Forest, Braselton, GA.

Table 1. Allozyme loci resolved for *Amelanchier laevis* and *A. arborea*. Buffer systems are from Soltis et al. (1983), 4 = Electrode buffer: 0.223 M Tris, 0.086 M citric acid, NaOH to pH 7.5; Gel buffer: 0.008 M Tris, 0.003 M citric acid, NaOH to pH 7.5; and 6 = Electrode buffer: 0.3 M boric acid, 0.1 M NaOH; Gel buffer: 0.015 M Tris, 0.003 M citric acid.

	Number of Alleles		
Locus	*A. laevis*	*A. arborea*	Buffer System
Aco	1	1	4
Fe-1	1	1	6
Lap	1	1	6
6-Pgd-1	2	2	4
6-Pgd-2	1	2	4
Pgi	2	3	6
Tpi-1	2	3	6
Tpi-2	1	1	6
Tpi-3	3	3	6
Tpi-4	1	4	6

starch gel electrophoresis, we resolved ten loci (Table 1) with standard recipes (Soltis et al. 1983).

We estimated the amount of genetic variation at the population and species level with the following parameters: percent polymorphic loci (P), effective number of alleles per locus (A_e), mean number of alleles per polymorphic locus (AP), and expected heterozygosity (H_e; Nei 1973). In order to estimate departure from Hardy-Weinberg expected frequencies, we also calculated observed heterozygosity (H_o) and Wright's fixation index (F) for each polymorphic locus in every population. The significance of non-zero fixation indices was tested with chi-square tests (Li and Horvitz 1953). We calculated Nei's (1973) genetic diversity statistics—total genetic diversity (H_T), mean diversity within populations (H_S), and proportion of diversity among populations (G_{ST})—over polymorphic loci to estimate variation among populations. We also estimated gene flow using the indirect methods of Wright (1951) and Slatkin (Barton and Slatkin 1986; Slatkin 1985). These statistics were calculated by a computer program (LYNSPROG) developed by M. D. Loveless and A. F. Schnabel (available from J. L. H.). We generated a UPGMA phenogram of genetic identities among all populations using NTSYS (Rohlf 1988). We also estimated multilocus genotype diversity within populations of both species by counting the number of multilocus genotypes and computing the modified Simpson index (Pielou 1969) used by Ellstrand and Roose (1987) and more recently by Sherman-Broyles et al. (1992).

RESULTS

Although reports of tetraploids occur for both species and maloids are of polyploid origin, we saw no evidence of tetrasomic inheritance for any of the 10 loci sampled. Some enzyme systems were obviously, as expected, encoded by several loci (*Fe*, *Pgd*, and *Tpi*) and formed interlocus-heterodimers, which can be difficult to interpret. However, all loci exhibited patterns that could be interpreted with relative ease as being due to diploid inheritance. [A few loci, such as Fe-2, were not scored because they could not be read consistently. In hindsight, we might have resolved more loci by using a different extraction protocol; Overath and Kawahara (unpublished data) resolved more than 20 loci from *Amelanchier asiatica* (Sieb. & Zuc.) Endl. using a slightly different extraction buffer and grinding without liquid nitrogen.]

Genetic variation in *Amelanchier laevis* was comparable to that in *A. arborea* (Table 2). At the species level, *A. laevis* had fewer alleles per polymorphic locus (2.25 vs. 2.80 in *A. arborea*), and lower effective number of alleles per locus (1.16 vs. 1.21) and expected heterozygosity (0.090 vs. 0.116). The percent of polymorphic loci was also lower in *A. laevis* (40% vs. 60%). The same trends were seen in measures of within population variation; however, the ranges of individual population values for the two species overlap extensively. Percent polymorphic loci ranged from 20% to 30% (mean = 24%) in *A. laevis* populations and from 20% to 60% (mean = 40%) in *A. arborea* populations. The mean number of alleles per polymorphic locus ranged from 2.00 to 2.33 in *A. laevis* (mean = 2.07) and from 2.00 to 3.00 in *A. arborea* (mean = 2.35). Finally, the effective number of alleles per locus for *A. laevis* ranged from 1.07 to 1.19 (mean = 1.14) and from 1.14 to 1.22 (mean = 1.18) for *A. arborea*.

Average expected heterozygosity was also lower in populations of *Amelanchier laevis* (0.080 vs. 0.100 in *A. arborea*); however, average observed heterozygosity was slightly higher (0.071 vs. 0.066). Observed heterozygosity was lower than expected heterozygosity for both species. Consistent with the low observed het-

Table 2. Summary of allozyme diversity for ten loci within five populations of *Amelanchier laevis* and four populations of *A. arborea*. P = proportion of polymorphic loci, AP = mean number of alleles per polymorphic locus, A_e = effective number of alleles, H_o = mean observed heterozygosity, H_e = mean expected heterozygosity.

Population	Sample Size	P(%)	AP	A_e	H_o (s.d.)	H_e (s.d.)
A. laevis						
1L	30	30	2.33	1.19	0.075 (0.015)	0.101 (0.064)
2L	22	20	2.00	1.16	0.093 (0.020)	0.086 (0.060)
3L	44	20	2.00	1.17	0.086 (0.013)	0.092 (0.062)
4L	48	30	2.00	1.11	0.056 (0.011)	0.066 (0.048)
6L	17	20	2.00	1.07	0.041 (0.015)	0.054 (0.062)
Mean		24	2.07	1.14	0.071 (0.007)	0.080 (0.025)
Species level		40	2.25	1.16	—	0.090
A. arborea						
5A	48	60	2.00	1.22	0.086 (0.013)	0.118 (0.063)
7A	31	30	2.00	1.16	0.053 (0.013)	0.092 (0.057)
8A	48	50	2.40	1.20	0.094 (0.013)	0.112 (0.062)
9A	38	20	3.00	1.14	0.029 (0.009)	0.078 (0.054)
Mean		40	2.35	1.18	0.066 (0.006)	0.100 (0.030)
Species level		60	2.80	1.21	—	0.116

erozygosity, 6% of the fixation indices (F) for *A. laevis* and 17.5% for *A. arborea* were significantly greater than zero ($P \leq 0.05$).

Total genetic diversity at polymorphic loci (H_T) was higher for *Amelanchier laevis* (0.225 vs. 0.193 for *A. arborea*) indicating that allele frequencies were more skewed in *A. arborea*. Mean diversity within populations (H_S) was essentially equal for these two species (0.205 for *A. laevis* and 0.203 for *A. arborea*). Both species also had little genetic differentiation among populations (*A. laevis*, $G_{ST} = 0.054$ and *A. arborea*, $G_{ST} = 0.057$). Consequently, gene flow estimates were high for these species. Wright's estimate of gene flow was 4.41 migrants per generation for *A. laevis* and 4.17 migrants per generation for *A. arborea*. Slatkin's estimate for *A. laevis* was 12.58 migrants per generation [three private alleles, $\bar{p}(1) = 0.018$] and for *A. arborea* was 6.42 [four private alleles, $\bar{p}(1) = 0.020$].

Among *Amelanchier laevis* populations, genetic identities ranged from 0.96 to 1.00 with a mean of 0.98. Populations 3L and 2L, two of the Maine populations, were most similar and 3L

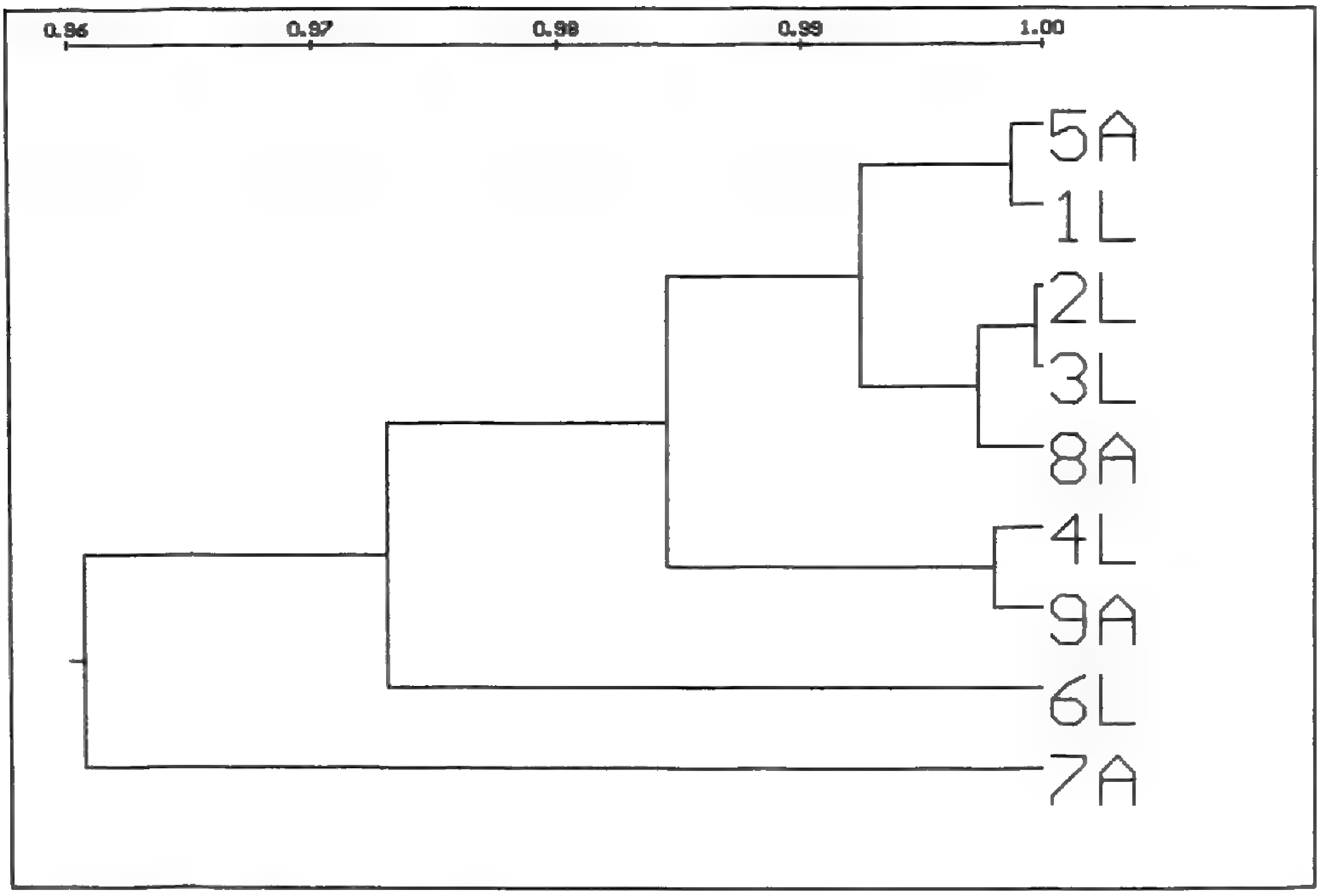

Figure 2. Phenogram of Nei's genetic identities for all nine *Amelanchier* populations. Letters after the numbers refer to the species: L = *A. laevis*, A = *A. arborea*. Locations are defined in Figure 1.

and 6L, the Virginia population, were the least similar. Genetic identities among *A. arborea* populations were similar, ranging from 0.93 to 1.00 with a mean of 0.97. The most similar *A. arborea* populations were 5A and 8A, the Pennsylvania and North Carolina populations, while the least similar were 7A and 9A, the Virginia and the Georgia populations. Genetic identity between the two species was 0.997. *Amelanchier arborea* had five alleles not found in *A. laevis* (one each at *6-Pgd-2* and *Tpi-1*, and three at *Tpi-4*). Considering all populations together (Figure 2), the two Virginia populations, 6L and 7A, were the least similar to the other populations. In all cases, *A. arborea* populations were more similar to an *A. laevis* population than to other *A. arborea* populations. *Amelanchier laevis* populations were also more similar to populations of *A. arborea* except in the case of 3L and 2L, two of the Maine populations.

The number of multilocus genotypes (MLG) per population for *Amelanchier laevis* ranged from 5 to 10 (mean = 7.4) and from 9 to 16 (mean = 12.8) for *A. arborea*. Since *A. laevis* populations tended to be smaller, differences could be due merely to sample size. When corrected for sample size (MLG/N; Table 3), *A. laevis*

Table 3. Number of multilocus genotypes (MLG), number of multilocus genotypes corrected for sample size (MLG/N), genotypic diversity indices (Dg), and probability of the most common genotype (MCG) for five populations of *Amelanchier laevis* and four populations of *A. arborea*.

Population	Sample Size	MLG	MLG/N	D_g	MCG
A. laevis					
1L	26	10	0.385	0.89	0.21
2L	19	7	0.368	0.84	0.24
3L	44	8	0.182	0.86	0.22
4L	47	7	0.149	0.77	0.35
6L	17	5	0.294	0.58	0.54
Mean (s.d.)	30.6 (14.0)	7.4 (1.81)	0.276 (0.11)	0.79 (0.12)	0.31 (0.14)
A. arborea					
5A	45	16	0.356	0.90	0.16
7A	28	9	0.321	0.87	0.29
8A	45	16	0.356	0.92	0.20
9A	38	10	0.263	0.78	0.35
Mean	39 (8.0)	12.8 (3.8)	0.324 (0.04)	0.87 (0.06)	0.25 (0.09)

still had fewer MLG's; however, the corrected values overlap more extensively than the uncorrected values. The corrected values ranged from 0.149 to 0.385 (mean = 0.276) for *A. laevis* and 0.263 to 0.356 (mean = 0.324) for *A. arborea*. Genotypic diversity indices ranged from 0.58 to 0.89 (mean = 0.79) and from 0.78 to 0.92 (mean 0.87) for *A. laevis* and *A. arborea*, respectively. The probability of the most common genotype per population for each species ranged from 0.21 to 0.54 (mean = 0.31) for *A. laevis* and from 0.16 to 0.35 (mean = 0.25) for *A. arborea*.

DISCUSSION

Overall, levels and distribution of genetic diversity in *Amelanchier laevis* and *A. arborea* are similar. Although *A. arborea* has more polymorphic loci and somewhat higher expected heterozygosity and *A. laevis* has higher mean total genetic diversity (H_T) at polymorphic loci, other measures of genetic diversity are similar. Compared to other woody species, both *Amelanchier* species have less genetic diversity (H_e; Hamrick et al. 1992).

Both *Amelanchier laevis* and *A. arborea* also have within population genetic diversity values (H_e) between the averages for outcrossing-animal dispersed species and mixed mating-animal dispersed woody species (Hamrick et al. 1992). Similarly for both species, genetic diversity at the species level is comparable to mixed mating-animal dispersed species (Hamrick et al. 1992). Among *Amelanchier* species, sexuality is usually associated with self-incompatibility while facultative apomicts are apparently self-compatible (Campbell and Dickinson 1990; Campbell et al. 1985, 1987; Weber and Campbell 1989). Robinson (1982) tentatively concluded that *A. arborea* is self-incompatible. Campbell et al. (1985) stated that *A. laevis* is self-compatible; however, studies utilizing genetic markers are needed to determine whether any offspring are actually produced via selfing. Our data suggest that selfing may be possible in these species because some loci had a significant deficit of heterozygotes for both species (as indicated by the significantly positive fixation indices).

These two taxa have lower than average genetic diversity for woody species capable of both sexual and asexual reproduction or than is usual for sexually reproducing woody species (Hamrick et al. 1992). While it is possible that *Amelanchier* species in general have less allozyme diversity than is normal for woody species, a preliminary study of an Asian species (*A. asiatica*) over a very small geographic range in Japan found much higher levels of heterozygosity ($H_e = 0.130$ within populations, $H_e = 0.168$ at the species level; Overath and Kawahara, unpublished data). Perhaps DNA-based markers would reveal higher amounts of variation, as has been the case for *Rubus* spp. (Antonius and Nybom 1994; Nybom and Schaal 1990).

If the two American species had different ploidy levels, we might expect the polyploid to have more variation (Moody et al. 1993); however, as already mentioned, these species have both been identified as tetraploids (Campbell et al. 1985; Cruise 1964), although diploid counts have also been reported (Robinson and Partanen 1980). Since polyploidy is associated with apomixis in the Maloideae (Campbell et al. 1991), the ability to reproduce apomictically may be present and variable in both species. Maine populations of *Amelanchier laevis*, which are known to be polyploid and capable of apomixis (C. S. Campbell, pers. comm.), have slightly more genetic diversity than other *A. laevis* populations; however, no such north-south trend exists for *A. arborea*.

If ploidy and sexuality vary with latitude as Campbell et al. (1991) tentatively suggest, they have little effect on levels of allozyme diversity maintained within populations of these two species. Furthermore, for the allozyme loci sampled, we found no evidence of polysomic inheritance for either species; therefore, other methods such as chromosome counts, cytodensitometry (Campbell et al. 1989), or flow cytometry (De Rocher et al. 1990) over the range of these species will be necessary to resolve this issue. Studies using genetic markers to estimate mating systems would also be helpful in determining whether variation in sexuality occurs and whether it accompanies variation in ploidy level.

G_{ST} values for both species are low, indicating little genetic differentiation among populations. If most reproduction is asexual and plants are isolated, we might expect to see higher levels of population differentiation than in purely sexual species which, presumably, would have more gene flow, at least via pollen. However, G_{ST} is marginally lower and gene flow (Nm) is slightly higher in *Amelanchier laevis*, the only one of the two species in which apomixis has been documented. Furthermore, G_{ST} for both species is similar to the mean G_{ST} for woody species capable of both sexual and asexual reproduction ($G_{ST} = 0.051$; Hamrick et al. 1992). Not surprisingly, mean G_{ST} for species whose seeds are ingested is also similar (0.051; Hamrick et al. 1992). Fruits of *Amelanchier* are attractive to birds (Gorchov 1988), which may contribute to gene flow and, thereby, lower population differentiation. If seed migration is extensive, we would expect that populations of a highly apomictic species, for which seeds are clones, to be more similar than those of a sexual species.

Both *Amelanchier laevis* and *A. arborea* have fewer multilocus genotypes per population than the average for clonal species (mean = 16.1; Ellstrand and Roose 1987), but higher indices of genotypic diversity (Dg = 0.62; Ellstrand and Roose 1987). Most of the species Ellstrand and Roose (1987) considered were not apomictic; however, if we consider only the apomictic species, the trends stay the same (mean MLG = 29.1 and Dg = 0.58). Ellstrand and Roose (1987) also found that sampling additional polymorphic loci increased the number of multilocus genotypes per population. Since the number of loci resolved (10) and genetic diversity at these loci are relatively low, clonal diversity may be underestimated. In any case, *A. laevis* has approximately half the number of multilocus genotypes as *A. arborea*, which is a sexual species in at least part of its range (Michigan; Gorchov 1988). However, this difference is due mainly to larger sample sizes (due to larger population sizes) for *A. arborea* as indicated by the ratio of multilocus genotype/sample size (MLG/N; Table 3).

When comparing genetic identity values, we find that these two taxa are highly similar (I = 0.997). Populations within each species also have high genetic identities as do populations of both taxa combined. In fact, most populations of *Amelanchier laevis* are more similar to *A. arborea* populations than to other populations of *A. laevis* (Figure 2). If ploidy levels and/or sexuality vary among populations in these species, perhaps those populations that group together are of the same ploidy level. Dickson et al. (1991) explained high genetic identities among three *Malus* taxa (I = 0.983 to 0.996) as a possible example of rapid speciation because morphological divergence may have occurred faster than that of allozymes. Similar types of evidence are emerging for other groups of species in which hybridization is extensive (Hodges and Arnold 1994).

In mixed populations of these two *Amelanchier* species, Cruise (1964), using a hybrid index, found more than 25% of the individuals had intermediate morphological characters. He suggested that *A. arborea* and *A. laevis* should be combined with a third species, *A. canadensis* (L.) Medikus, in which apomixis has been documented (Campbell et al. 1987). Genetic identities between these taxa and others in the genus would be useful in gauging similarity among *Amelanchier* species in general. If genetic identities between *A. laevis* and *A. arborea* prove to be high compared to those of other congeners, Cruise's (1964) proposal to combine these two species would be warranted. If, however, *Amelanchier* species in general have high genetic identities, perhaps these species have recently undergone a rapid morphological divergence, as has been proposed for *Malus* (Dickson et al. 1991) and other plant species (Hodges and Arnold 1994). A less likely explanation, if these species are predominantly apomictic throughout their range, is that widespread hybridization may prevent species divergence.

If these two species differ in mating system, our results would support those of Dickinson and Campbell's (1991) morphological study of *Amelanchier laevis* and *A. bartramiana* (Tausch) Roemer. *Amelanchier laevis*, the facultative apomict, has slightly lower, but basically comparable, amounts of variation than that in its sexual congener. However, recently in a more extensive study, Campbell et al. (1997) found that the sexual species had more morphological variation, although, as in our study, the distribution of variation among populations did not differ.

Because sexuality may vary within both taxa, more in-depth studies of *Amelanchier* species, including documentation of mating systems for each population, are needed. Geographic variation in sexuality would make *Amelanchier* ideal for studying the effects of facultative apomixis within a single taxon by comparing totally sexual and facultatively apomictic populations. In addition, studies of the amounts of apportionment of variation, as measured by genetic markers such as allozymes, for other *Amelanchier* taxa are needed to ascertain whether the high genetic identity between *A. laevis* and *A. arborea* is due to the fact that these two species should be merged or that little genetic differentiation among congeners is characteristic of this genus.

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NOTES ON *CAREX AZUAYAE* AND *C. ENNEASTACHYA* (CYPERACEAE) FROM SOUTH AMERICA

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ABSTRACT. *Carex enneastachya* is the only member of section *Phacocystis* thus far known from northern South America. *Carex azuayae*, originally described from Ecuador, is here considered to be conspecific with *C. enneastachya*. Additionally, this note represents the first report of *C. enneastachya* from Bolivia.

Key Words: Bolivia, *Carex enneastachya*, *Carex* sect. *Phacocystis*, Colombia, Cyperaceae, Ecuador

Carex L. (Cyperaceae) is well represented worldwide, and it has been estimated that over 200 species occur in South America (Wheeler 1996). Sectional representation, however, can vary greatly from one continent to another. For instance, many members of *Carex* section *Phacocystis* Dumort. are known from North America (Mackenzie 1935; Standley 1985, 1987b) and Eurasia (Charkevicz 1988; Chater 1980), but less than ten species are recognized from South America (Barros 1947; Clarke 1908; Jørgensen and Ulloa Ulloa 1994; Kükenthal 1909; Marticorena and Quezada 1985; Steyermark 1964). Moreover, out of the last group, only two species, *C. azuayae* Steyerm. and *C. enneastachya* C. B. Clarke, have been reported from the northern half of the continent. In this paper *C. azuayae*, which was originally described from Ecuador (Steyermark 1964), is considered to be conspecific with *C. enneastachya*, whose type collection comes from Colombia (Clarke 1908) and whose name has priority. In addition, *C. enneastachya* is here reported for the first time from Bolivia.

MORPHOLOGY AND DISCUSSION

Clarke (1908, p. 70) described *Carex enneastachya* from plants collected in Colombia and noted its apparent relationship to the Eurasian *C. acuta* L. (sect. *Phacocystis*). The holotype is characterized by having: leaves rather narrow (average width 2.8

mm); an inflorescence with 10 elongate, erect spikes; lowest bract much exceeding the inflorescence; perigynia stipitate (stipe 4–6 mm long), the body elliptic to broadly elliptical, minutely papillose, with 4–7 obscure nerves on each face; and achenes lenticular, with oval to obovate sides, and adnate to the spongy tissue filling the base of the perigynium. Although Clarke reported the holotype as having nine spikes, hence the epithet *enneastachya*, the single plant mounted on the herbarium sheet actually has 10 spikes, i.e., 4 staminate spikes (3 of which are appreciably smaller than the terminal spike) and 6 androgynous or pistillate spikes. As mounted on the type sheet, the smallest staminate spike is "hidden" beneath another lateral staminate spike, and it most likely was the one overlooked by Clarke.

In 1964, Steyermark (p. 337) described *Carex azuayae* from a collection made in Azuay Province in southern Ecuador and placed it in section *Phacocystis* (his section *Acutae*). He pointed out the affinities of *C. azuayae* to various North American and austral South American members of section *Phacocystis*, but made no mention of *C. enneastachya*. Steyermark noted that *C. azuayae* is characterized by having several (6–7) slender, elongate spikes, stipitate perigynia, and a lowermost bract that conspicuously exceeds the inflorescence. Moreover, both the F and US specimens (citations given below) have rather narrow leaves, minutely papillose perigynia, with 4–7 obscure nerves on each face, and oval to obovate lenticular achenes that are adnate to the spongy tissue filling the base of the perigynium. Indeed, an examination of type material of *C. enneastachya* and *C. azuayae* reveals that the two entities are conspecific, with the former name having priority. In this regard, it is notable that in a recent treatment of the seed plants of the high Andes of Ecuador, Jørgensen and Ulloa Ulloa (1994) used the name *C. azuayae* for the plants under consideration.

Because no English description of *Carex enneastachya* has previously been published, one is provided below.

Carex enneastachya C. B. Clarke, Bull. Misc. Inform., Add. Ser. 8: 70. 1908. TYPE: COLOMBIA. *Jameson 2* (HOLOTYPE: K!). [The exact locality and date of collection are unknown to me.]

Carex azuayae Steyermark, Phytologia 9: 337. 1964. TYPE: ECUADOR. Prov. Azuay: vicinity of Toreador, between Molleturo and Quinoas, alt. 3785–3900 m, 15 Jun 1943, *Steyermark 53105* (HOLOTYPE: F!; ISOTYPE: US!).

Plants rhizomatous; rhizomes 2–3 mm thick, brownish. Fertile culms 28–56 cm tall, erect, trigonous, smooth, phyllopodic, with glabrous, pale brown to brown basal sheaths. Leaves (3–) 5–9, mostly on lower one-third of culm; blades 10–45 cm long, 1.8–4.4 (–5) mm wide, flat or convolute, glabrous, the margins finely antrorsely scabrous (especially in the distal half); leaf sheaths 1.5–4.5 cm long, glabrous, pale brown to brown; inner band of sheaths hyaline or pale brown, minutely purplish brown dotted, concave at the apex; ligules 1.5–4 mm long, subacute, hyaline, minutely purplish brown dotted. Inflorescences 9–15.5 cm long, with the spikes usually all strongly overlapping except sometimes the lowest one, which is (2–) 3.3–5.2 cm distant; spikes single at nodes, erect, all on stiff, smooth or sparingly scaberulent peduncles; lowermost spikes with peduncles 1.5–5.5 mm long, the uppermost lateral spikes sessile or nearly so; lowermost bracts with blades 12–22 cm long and 1.5–2.5 mm wide and sheaths 0.5–1.1 cm long, generally exceeding the inflorescence, the uppermost bracts much reduced. Spikes 6–10, the upper 1–4 staminate, the rest androgynous or pistillate. Terminal spikes 2.5–3.2 cm long, 3–5 mm wide, ca. 80–120-flowered; peduncles 5–10 mm long. Lateral staminate spikes (when present) smaller than the terminal spike, 0.8–1.5 cm long, ca. 10–30-flowered (pistillate flowers may occur sporadically on staminate spikes). Lateral androgynous or pistillate spikes 2–5 cm long; when androgynous staminate portion up to 0.6 cm long and ca. 5–20-flowered; pistillate portion 1.7–5 cm long, 3–4.5 mm wide, ca. 40–150-flowered. Pistillate scales 1.9–2.4 mm long, 0.8–1.3 mm wide, elliptic or slightly obovate, obtuse, purplish brown with narrow hyaline border and green or stramineous center, 1-veined, with the single vein extending almost to the apex of the scale but rarely excurrent as an awn. Staminate scales 2.5–4 mm long, 1.2–1.8 mm wide, elliptic or slightly obovate, obtuse, purplish brown with narrow hyaline border and green or stramineous center, 1-veined, with the single vein extending almost to the apex of the scale but rarely excurrent as an awn. Perigynia 2.2–2.8 mm long, 1.2–1.6 mm wide, broader than subtending scales, minutely papillose, biconvex with elliptic to broadly elliptical sides, with 4–7 obscure nerves on each face, tawny, often purplish-tinged in the distal two-thirds of the body, stipitate (the stipe 0.4–0.6 mm long); perigynium beak 0.1–0.2 mm long, entire, purplish brown. Achenes 1.3–1.6 mm long, 1–1.4 mm wide, lenticular with oval to obovate sides, brown, adnate to spongy tissue filling base of perigynium. Stigmas 2. Anthers 3, 1.3–1.9 mm long.

ADDITIONAL SPECIMEN EXAMINED: **Bolivia.** Depto. La Paz, Prov. Nor Yungas: pasando Undauavi antes de llegar a Cotapata, subiendo la senda antigua hacia Coroico, 3500 m, 22 Oct 1994, *Beck 21499* (LBP, MIN).

Carex enneastachya is known from single collections in Bolivia, Colombia, and Ecuador. Although Beck's Bolivian collection has slightly immature perigynia and poorly developed achenes, the plants are clearly assignable to *C. enneastachya*, a species hitherto unknown from Bolivia. This species has been collected in páramo, at elevations from about 3500 to 3900 m, and grows in boggy and marshy places. In Bolivia the species apparently flowers in September and October, though in Ecuador plants with mature perigynia and ripe achenes have been collected in mid-June. The epithet *enneastachya*, which means literally "with nine spikes," is somewhat misleading because fertile culms of this species seem to bear anywhere from six to ten spikes. Moreover, as mentioned earlier, the single plant comprising the holotype actually has ten spikes.

This species appears to be most closely related to the *Carex lenticularis* Michaux complex of the Western Hemisphere, whose members are characterized by having perigynia that are weakly nerved, minutely papillose, and stipitate, with the proximal spongy-thickened tissue of the perigynium adnate to the base of the achene (Standley 1985, 1987b). Also, what Steyermark (1964, p. 338) called a "reticulate surface" in the achene of *C. enneastachya* (as *C. azuayae*) most likely is a "layer of translucent or iridescent cells," as reported by Standley (1985, p. 60) in *C. lenticularis s.l.* In addition to *C. enneastachya*, other Latin American members of this complex include: *C. decidua* Boott, which ranges from Tierra del Fuego northward to northern Patagonia and is also disjunct on the Falkland Islands (Barros 1947; Marticorena and Quezada 1985); *C. hermannii* Cochrane, a Mexican endemic with reportedly a restricted range (Cochrane 1981); and *C. cuchumatanensis* Standl. & Steyerm. from Guatemala. According to Standley (1987a, p. 13), these three last-mentioned species "form a cohesive group based on anatomical and micromorphological characters." Regarding the geography of this complex, *C. enneastachya* is critically situated between the species of Central America and the southern Andes.

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A COMPARISON OF THE SEED BANKS OF SAND DUNES WITH DIFFERENT DISTURBANCE HISTORIES ON CAPE COD NATIONAL SEASHORE

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ABSTRACT. The seed bank compositions of four different coastal sand dunes on Cape Cod National Seashore (Massachusetts, USA) were characterized and used to predict the potential of seed banks in restoring species diversity in degraded sand dunes. Seedling emergence from sand collected from each site was observed over 15 weeks. A total of 254 seedlings emerged during the study. A single species, *Artemisia caudata*, was responsible for 85% of the total seedling emergence, and all but one of those seedlings was from a single study site. Overall, seedling emergence and the species diversity of seedlings was low, indicating a low density of seeds in the sand dune substrate. Seedlings emerged from only 20% of the sand samples, indicating that the distribution of seeds in the sand is tightly clustered. The lowest numbers of seedlings emerged from the most severely degraded site which had recently been replanted with *Ammophila breviligulata* (American Beachgrass). Potential reasons for this clumping of seedlings are discussed, including poor seed dispersal as a result of buried mature infructescences or as a result of wind deposition of seeds in small depressions. The results suggest that the existing seed bank is unlikely to lead to significant increases in species diversity at sites undergoing restoration. Consequently, the importation of sand and its associated seed bank from more mature sites is not a feasible means of restoring diversity because of the low density and species diversity of seeds in the sand at more stable sites.

Key Words: Cape Cod National Seashore, disturbance history, sand dune ecology, seed bank

Soil seed banks play important roles in plant community dynamics. Buried seeds provide a source of new recruits into plant populations and can greatly influence the species composition and density of individuals in a community, especially following a disturbance event. Some species may persist in the seed bank in a dormant, but viable, state for hundreds of years before proper conditions for germination and emergence return them to the adult community (Baker 1989). During the dormancy period, substantial changes in the community composition may have oc-

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curred. Previous studies have found that the composition and abundance of species in the soil seed bank do not necessarily reflect the composition and abundance of aboveground adults in the same area (Major and Pyott 1966; Thompson and Grime 1979; Whipple 1978). However, frequently disturbed areas often show a close correlation between adult vegetation and the soil seed bank (Henderson et al. 1988). In addition to their ecological and evolutionary significance (reviewed in Fenner 1985, 1992; Leck et al. 1989), soil seed banks may also have important implications for habitat conservation and management (Keddy et al. 1989). Soil seed banks have been used successfully in restoration of abandoned surface coal mines (Johnson and Bradshaw 1978). Van der Valk and Pederson (1989) have reviewed the use of seed banks in habitat restoration and suggest that soil seed banks have great potential for the restoration of degraded habitat.

The plant communities of Cape Cod, Massachusetts, have experienced severe anthropogenic disturbance since European colonization of New England and much effort has been devoted to their restoration. Extensive logging and grazing resulted in almost complete deforestation of the outer Cape (Eastham, Wellfleet, Truro, Provincetown) by the early 1800s (Westgate 1904). Removal of the vegetation caused extensive sand erosion. Fierce winter winds, rain, and snow began moving and shaping the bare sand dunes that still exist today. Sand control efforts in the Province Lands of the outer Cape began in 1825 when the moving sand not only buried homes but also threatened Provincetown's greatest economic asset, the harbor (Hawk and Sharp 1967; Westgate 1904). American Beachgrass, *Ammophila breviligulata*, was found to be the only plant that could survive in the moving sand and effectively stabilize it. Although large expanses of planted *A. breviligulata* to some extent have now stabilized sand dunes, these replantings have not re-created the biodiversity of undisturbed dunes which support a greater diversity of species. Stabilized areas that receive gradual sand accumulations may be colonized by annuals such as *Cakile edentula* and *Xanthium echinatum* Murr. and herbaceous perennials such as *A. breviligulata, Solidago sempervirens, Artemisia caudata*, and *Lathyrus japonicus* (Stalter 1993). Shrubs such as *Hudsonia tomentosa, Arctostaphylos uva-ursi* (L.) Spreng., *Myrica pensylvanica, Rosa rugosa*, and *Prunus maritima*, and finally, trees such as *Pinus rigida*

Miller and *Quercus* spp. may invade and eventually dominate the areas.

In 1963 the Cape Cod National Seashore (CCNS) took over the role of sand control on most of the outer Cape. Extensive efforts have been undertaken to restore the degraded coastal sand dune ecosystems within the boundaries of the CCNS. *Ammophila breviligulata*, a clonal perennial grass with spreading rhizomes, has been planted extensively with the primary goal of stabilizing the moving sand. Other methods have been examined such as the addition of inorganic fertilizer and inoculation of the soil with mycorrhizal fungi (Koske and Gemma 1992) in order to improve the vigor of *A. breviligulata* plantings. The potential for existing seed banks to promote natural succession and revegetation of the sand dunes has not been examined, however. We propose that sand dunes that have been disturbed and replanted with *A. breviligulata* have a lower species richness and buried seed density than those dunes that have experienced less human disturbance. In this study, we examine the composition and abundance of species in the seed bank of four sand dunes on Cape Cod National Seashore with different past disturbance and recovery histories. Due to the unique disturbance history and recovery of each site, each site is evaluated individually and then compared with each other site. The data will be used to predict the potential for the seed banks at replanted sites to increase species diversity in the future, and the potential for seed banks from undisturbed sites to be used in restoring degraded sites.

MATERIALS AND METHODS

Field sites. All study sites were located in backdune areas dominated by *Ammophila breviligulata* within the boundaries of Cape Cod National Seashore, Massachusetts, USA. The study sites consisted of two areas that had been replanted with *A. breviligulata* following severe anthropogenic disturbance and two areas that had received little human disturbance and had never been replanted.

The High Head site (42°15′N, 70°10′W) is located east of Pilgrim Lake in the town of Truro. Severe anthropogenic disturbance has destroyed much of the vegetation on the sand dunes adjacent to Pilgrim Lake. Unlike all the other sites, which are adjacent to beaches, this site is in a depression behind parabolic secondary dunes that are moving in a southeasterly direction at a rate of 10–20 ft. per year toward Pilgrim Lake (Madore and Leatherman 1981). The sampling site gradually rises up from the bottom of the depression at a 10–20% grade. In an effort to stabilize the moving sand, the area was planted with rows of nursery-raised *Ammophila breviligulata* in 1989 (Koske and Gemma 1992).

The Marconi Station site is due east of the water tower near the CCNS headquarters in South Wellfleet, between Marconi Beach and the Guglielmo Marconi Memorial (41°55′N, 69°59′W). This area was subject to heavy military activity until 1963 when CCNS was established and was subsequently bulldozed and replanted with *Ammophila breviligulata* and allowed to revegetate naturally over the past three decades (David Crary, National Park Service, Fire Management Officer, pers. comm.). A three-year study has recorded negligible sand movement at this relatively flat site (Shumway, unpubl. data). A rapidly and severely eroding 20 m high cliff separates the beach from the study site, possibly reducing the deposition of new sand characteristic of many backdunes.

The Coast Guard Beach site is located south of the Coast Guard Environmental Education Center between Nauset Marsh and Coast Guard Beach in Eastham (41°45′N, 69°55′W). This barrier beach system, which experiences stochastic overwash events, is situated between an ocean beach and a salt marsh that is flooded by an inlet located further south. Because of rising sea levels and oceanic storms, this relatively flat area is undergoing "retreat," pushing the Coast Guard barrier beach westward onto the salt marsh (Godfrey 1979). An aerial photo taken on 12 September 1970 (CCNS aerial photo #8207, D. Crary, pers. comm.) shows that the location of the sampling site was actually part of the salt marsh at that time. The site experienced a number of anthropogenic disturbances until 1978 when the parking lot located adjacent to the site was destroyed by a winter storm. Since then, CCNS has curtailed foot traffic to prevent further erosion and protect nesting shore birds. This site represents a young dune system that has been vegetated naturally and thus will be considered a control in this study.

The Duck Harbor site (41°57′N, 70°04′W) is located north of Great Island in Wellfleet. The site, located between the beach overlooking Cape Cod Bay and a freshwater spring, occupies a total width of approximately 150 m. Because the primary dune separating the beach and the backdune area is only about 3 to 5 m high, this site has a gradual incline of 10–20% and is likely to receive considerable sand deposition (T. Baptista, pers. obs.). Aerial photos of Duck Harbor from 1938, 1960, 1974, and 1987 do not show any significant differences in the shape and extension of the dunes (CCNS library collection). Hand-drawn maps from 1856 (CCNS library) show that Duck Harbor beach was open to the ocean and connected to a small river system that extended inland. Sand deposition closed off the harbor about 120 years ago. An off-road vehicle trail through the site was closed about ten years ago and the site presently receives moderate foot traffic (D. Crary, pers. comm.). There is no evidence that the area has ever been replanted.

Seed bank characterization. Seed bank composition was determined for each site by observing seedling emergence from field-collected substrate samples. Direct determination of the seed bank composition was also attempted by sifting substrate samples with sieves of decreasing mesh sizes followed by suspending the organic matter in saline solutions. These methods proved ineffective because of poor and variable recovery rates (data not included) and will not be discussed further. See Roberts (1981) and Gross (1990) for discussions of standard methods for seed bank determinations.

Substrate samples from High Head, Duck Harbor, and the Marconi Station were collected on 13 March 1994 and from Coast Guard Beach on 20 March 1994. Substrate samples were collected in late winter after buried seeds had been exposed to a natural cold stratification period. Previous studies have found that soils exposed to seasonal chilling yield more seedlings than samples collected before winter (Leck and Graveline 1979; Raynal and Bazzaz 1973).

Samples were removed from a cylindrical core with a depth of 10 cm and diameter of 15 cm for a total volume of 1767 cm^3. At each site, one sample was collected every 10 m along each of four 100 m long parallel transects (10 m apart) using a stratified sampling method (Hutchings 1991) for a total of 40 samples per site.

In the germination experiment, 38 substrate samples from each site (because of greenhouse space constraints two random samples from each site were discarded) were each spread out in 25 cm × 25 cm × 6 cm plastic trays containing a 3 cm deep layer of potting soil for a total depth of 5 cm. The addition of the potting soil layer (Peters Professional "Redi Earth" potting soil and seed starting mix) increased the sample volume and helped to slow the rate of dessication of the thinly spread samples. Replicates were misted daily with tap water. Room temperature was maintained at 25–30°C. Banks of forty-watt wide-spectrum grow-lights positioned 15 cm above the samples provided a photoperiod of 16 hr. of light per day. The trays were examined for newly emerging seedlings at weekly intervals for 15 weeks. Upon identification the seedlings were removed from the trays. Trays were randomized on the greenhouse bench after each census in order to account for possible variations in ambient conditions (e.g., temperature, light intensity, etc.).

Adult vegetation survey. In order to compare aboveground vegetation with the seed bank at each site, adult species composition and density were determined along the same transects at each site on 22 May 1994. A 0.50 × 0.50 m quadrat was placed every ten meters and stem density (stems/0.25 m^2) was recorded for each species present. In order to more fully measure species richness we also recorded the identity and estimated the relative abundance (Dominant > Abundant > Frequent > Occasional > Rare; Mueller-Dombois and Ellenberg 1974) of all species that were observed growing at each site.

RESULTS

Seed bank characterization. A total of 254 seedlings emerged over the 15-week experiment in only 20% of the 152 samples (see frequencies in Table 1), indicating a highly clumped distribution of seeds in the sand. Eighty-nine percent of the seedlings originated from the Duck Harbor site. The Marconi Station and Coast Guard Beach sites were each responsible for 5%, and the High Head site contributed only 0.8%, of the total seedling emergence (Table 1). There was a statistically significant difference in the total number of seedlings emerging across the sites ($\chi^2 = 709.76$, $p < 0.001$).

The most common species in the seedling emergence experiment (85%) was *Artemisia caudata*. Of the 217 *A. caudata* seedlings that emerged, all but one originated from Duck Harbor sam-

Table 1. Results of the seed bank characterization experiment for each study site (N = 38). Top value = total number of seedlings emerging across all replicates. Middle value = mean (±SD) number of seedlings emerging per replicate. Bottom value = the frequency of seedling emergence in replicates (number of replicates in which seedlings emerged/total number of replicates × 100%). *$p < 0.05$, chi-square test comparing seedling emergence across study sites.

Species		High Head	Marconi Station	Coast Guard Beach	Duck Harbor
Ammophila breviligulata	*	1	6	6	0
		0.03 ± 0.16	0.16 ± 0.82	0.16 ± 0.68	0
		3	5	5	0
Artemisia caudata	*	0	0	1	216
		0	0	0.03 ± 0.16	5.7 ± 19.4
		0	0	3	29
Chenopodium rubrum		0	1	2	1
		0	0.03 ± 0.16	0.05 ± 0.23	0.03 ± 0.16
		0	3	5	3
Hudsonia spp.		0	2	0	0
		0	0.05 ± 0.23	0	0
		0	5	0	0
Solidago sempervirens		0	3	1	4
		0	0.08 ± 0.27	0.03 ± 0.16	0.10 ± 0.50
		0	8	3	5
Other species		1	1	2	6
		0.03 ± 0.16	0.03 ± 0.16	0.05 ± 0.23	0.15 ± 0.43
		3	3	5	13
Total	*	2	13	12	227
		0.05 ± 0.23	0.34 ± 1.07	0.32 ± 0.84	5.97 ± 19.8
		5	16	18	44

ples. Eighty-seven percent of the *A. caudata* seedlings emerged from three replicates and the remainder from eight other replicates. When *A. caudata* was removed from the data, differences in seedling emergence among the four sites still remained statistically significant ($\chi^2 = 8.11$, $p < 0.05$). The second most common seedling species, *Ammophila breviligulata*, emerged in the High Head, Marconi Station, and Coast Guard Beach samples, making up 5% of the total number of seedlings.

Solidago sempervirens, which made up 3% of all seedlings, emerged at all the sites except High Head. All together, the *Chenopodium rubrum* L., *Hudsonia* spp., *Artemisia stelleriana*, *Cakile edentula*, and *Polygonella articulata* seedlings made up less than 2% of all seedlings (the latter three species are listed under the "Other Species" category in Table 1).

Adult vegetation survey. *Ammophila breviligulata* was clearly the numerically dominant adult species at all four sites; however, it differed in abundance between sites (Table 2). The lowest *A. breviligulata* stem densities were found at the replanted sites with 10.2 ± 3.7 and 12.6 ± 5.8 (X ± S.D.) stems/0.25 m^2 at High Head and the Marconi Station, respectively. Duck Harbor averaged 23.1 ± 11.0 stems/0.25 m^2 and Coast Guard had the highest density of 37.4 ± 14.2 stems/0.25 m^2. *Ammophila breviligulata* was the only species to occur in 100% of the quadrats at all four sites. *Solidago sempervirens* was the second most abundant species at Marconi Station and Duck Harbor, yet averaged less than 3.2 individuals/0.25 m^2 and had a frequency of occurrence of less than 67%. Each of the other species averaged fewer than 1.9 individuals/0.25 m^2 and appeared in quadrats with a frequency of less than 46% (Table 2).

Marconi Station, Duck Harbor, and Coast Guard Beach had similar adult species richness with 9, 11, and 12 species, respectively (Table 3). *Ammophila breviligulata* and *Solidago sempervirens* were consistently the most abundant species at these sites. In marked contrast, High Head supported only *A. breviligulata* and the annual *Polygonella articulata*.

DISCUSSION

The seed banks at all four sand dune study sites are characterized by low species richness, low densities of viable seeds, and highly clumped distributions of seeds within the soil. The average

Table 2. Results of the adult vegetation survey for each study site (N = 40). Top value = the mean density (±SD) of adults/0.25 m^2 at each site. Bottom value = the frequency of occurrence of each species (number of quadrats containing the species/40 × 100%).

Species	High Head	Marconi Station	Coast Guard Beach	Duck Harbor
Ammophila breviligulata	10.2 ± 3.7 100	12.6 ± 5.8 100	37.4 ± 14.2 100	23.1 ± 11.0 100
Artemisia caudata	0 0	0 0	0 0	0.48 ± 1.3 13
A. caudata seedling	0 0	0 0	0 0	0.30 ± 1.2 8
A. stellariana	0 0	0 0	0.41 ± 1.8 5	0 0
Cakile edentula	0 0	0 0	1.9 ± 3.1 46	0 0
Carex sp.	0 0	1.1 ± 3.2 15	0 0	0 0
Lathyrus japonicus	0 0	0 0	0.51 ± 1.8 (0.18) 18	1.2 ± 2.6 25
Polygonella articulata	0.05 ± 0.32 3	0.05 ± 0.22 5	0.03 ± 0.16 3	0 0
Solidago sempervirens	0 0	3.2 ± 3.4 (0.67) 67	0 0	1.4 ± 4.2 40
S. sempervirens seedling	0 0	0.05 ± 0.22 5	0.13 ± 0.52 10	0.08 ± 0.35 5
Other species	0 0	0 0	0.10 ± 0.64 5	0.03 ± 0.16 3

total seedling emergence for Duck Harbor was 5.97 seedlings/ 1767 cm^3 and ranged from 0.05–0.34 seedlings/1767 cm^3 for the other three sites. For High Head, Coast Guard Beach, and the Marconi Station sites this is equivalent to approximately 3–20 seedlings/m^2 of surface area. Even this is a generous estimate based on the surface area collected by the cylindrical sampling device (15 cm diameter × 10 cm depth) and is based on the unrealistic assumption that all seeds to a depth of 10 cm are capable of germination. The paucity of seeds in the soil may be the result of poor seed production, intense pre- or post-dispersal seed predation (Louda 1989), pathogen attack, short seed lifespan, transport of seeds out of the dune habitat, or deep burial of seeds. However, little is known about the role of any of these factors in coastal sand dune communities (Ehrenfeld 1990; Maun 1985). Even less is understood about seed bank processes in backdune regions as most studies of sand dune seed ecology have focused on the foredune and strandline (Ehrenfeld 1990).

The predominant dispersal mode in sand dune species is wind (Ehrenfeld 1990) which is commonly associated with long-distance transport of seeds. Primary and secondary dispersal by wind can deposit seeds in favorable microsites or have the undesired effect of removing seeds from the system by dispersing them beyond suitable sand dune growing sites. Few studies have been conducted on seed dispersal in sand dune plants. Surprisingly, several studies of sand dune plant species have reported short-distance dispersal of seeds to locations close to parent plants (reviewed by Ehrenfeld 1990). Trapping of seeds by vegetation and settlement in depressions in the sand may influence the final resting places of wind-dispersed seeds. Such trapping effects can produce a clumped distribution of seeds in the seed bank and we have observed concentration of seeds in depressions soon after release from parent plants. However, this surface pattern becomes less obvious over time. We have also observed clusters of seedlings emerging from buried infructescences of *Ammophila breviligulata*, *Artemisia caudata*, and *Solidago sempervirens* and believe that burial of infructescences that have not released all their seeds may be an important determinant of clustering of seeds in the seed bank. These two processes most likely explain the highly clumped pattern suggested by our seed bank study.

There is a poor correlation between adult abundance and species representation in the sand dune seed bank. *Ammophila brev-*

Table 3. Relative abundance of all adult species found at each study site.

Species	Common name	Family	Abundance
High Head			
Ammophila breviligulata Fern.	Beach Grass	Poaceae	Dominant
Polygonella articulata (L.) Meissner	Jointweed	Polygonaceae	Frequent
Marconi Station			
Ammophila breviligulata Fern.	Beach Grass	Poaceae	Dominant
Artemisia stelleriana Besser	Dusty Miller	Asteraceae	Occasional
Carex sp.	Sedge	Cyperaceae	Rare
Chrysopsis falcata (Pursh) Elliott	Sickle-leaved Golden Aster	Asteraceae	Frequent
Cyperus polystachyos Rottb.	Sedge	Cyperaceae	Occasional
Euphorbia polygonifolia L.	Seaside Spurge	Euphorbiaceae	Frequent
Hudsonia tomentosa Nutt.	Beach Heather	Cistaceae	Occasional
Myrica pensylvanica Loisel.	Northern Bayberry	Myricaceae	Frequent
Oenothera fruticosa L.	Sundrops	Onagraceae	Rare
Polygonella articulata (L.) Meissner	Jointweed	Polygonaceae	Occasional
Rosa rugosa Thunb.	Rugosa Rose	Rosaceae	Occasional
Solidago sempervirens L.	Seaside Goldenrod	Asteraceae	Abundant
Coast Guard			
Ammophila breviligulata Fern.	Beach Grass	Poaceae	Dominant
Artemisia stelleriana Besser	Dusty Miller	Asteraceae	Abundant
Cakile edentula (Bigelow) Hook.	Sea Rocket	Brassicaceae	Abundant
Lathyrus japonicus Willd.	Beach Pea	Fabaceae	Abundant
Phragmites communis Trin.	Common Reed	Poaceae	Rare
Polygonella articulata (L.) Meissner	Jointweed	Polygonaceae	Frequent
Rhus radicans L.	Poison Ivy	Anacardiaceae	Occasional
Rosa rugosa Thunb.	Rugosa Rose	Rosaceae	Occasional
Solidago sempervirens L.	Seaside Goldenrod	Asteraceae	Abundant

Table 3. Continued.

Species	Common name	Family	Abundance
Duck Harbor			
Ammophila breviligulata Fern.	Beach Grass	Poaceae	Dominant
Artemisia caudata Michx.	Wormwood	Asteraceae	Abundant
Artemisia stelleriana Besser	Dusty Miller	Asteraceae	Frequent
Hudsonia tomentosa Nutt.	Beach Heather	Cistaceae	Rare
Juncus greenei Oakes & Tuckerm.	Rush	Juncaceae	Frequent
Lathyrus japonicus Willd.	Beach Pea	Fabaceae	Abundant
Lechea sp.	Pinweed	Cistaceae	Frequent
Polygonella articulata (L.) Meissner	Jointweed	Polygonaceae	Occasional
Prunus maritima Marshall	Beach Plum	Rosaceae	Rare
Rosa rugosa Thunb.	Rugosa Rose	Rosaceae	Occasional
Solidago sempervirens L.	Seaside Goldenrod	Asteraceae	Abundant

iligulata was the numerically dominant species at all sites and represents the most abundant indicator species on the sand dunes of eastern North America north of the Carolinas. *Solidago sempervirens* was the second most abundant species at all sites except High Head, which had been replanted with *A. breviligulata*. Despite being the dominant adults, these two species were present in very low densities in the seed bank (< 9 individuals/m^2). In comparison, the greatest seedling emergence was by *Artemisia caudata* (335/m^2) at Duck Harbor, where its adult density averages only 1.9/m^2. These results indicate that adult species abundance may not be a good predictor of species representation in the seed bank. This conclusion is not unique to sand dune communities and has been noted for many other communities, particularly in wetlands dominated by adults with clonal growth morphologies (Baldwin et al. 1996; Leck 1989; Shumway and Bertness 1992).

Emerging seedling densities, adult densities, and species richness were markedly lower at the most recently replanted site (High Head) than at the other three sites (Table 1). Nine, eleven, and twelve different species of adults were observed at Coast Guard Beach, Duck Harbor, and Marconi Station, respectively, while High Head supported only two species of adults (Table 3). The two replanted sites, High Head and Marconi Station, supported *Ammophila breviligulata* densities that were 2 to 3 times lower than at Coast Guard Beach and Duck Harbor (Table 2). Despite the lack of historical human disturbance, Coast Guard Beach and Duck Harbor are located closer to the foredune and, as a result, probably receive greater input of sand and nutrient deposition from sea spray, which may increase growth in *A. breviligulata*. The lowest overall seedling diversity and seedling number was at the High Head site, which was replanted in 1989, suggesting that heavily disturbed, unstable areas (marked by significant erosion) have depauperate seed banks. The highest seedling emergence was at Duck Harbor and can be attributed to a single species. When *Artemisia caudata* is removed from the data, Duck Harbor has similar adult plant abundance and diversity of species in the seed bank as the Marconi Station and Coast Guard Beach, which have been in a state of recovery for over 30 and 10 years, respectively. Similarly, the difference in the total number of seedlings emerging across all sites remains significant without *A. caudata* in the data set ($\chi^2 = 8.77$, $p < 0.05$). Marconi

Station, Coast Guard Beach, and Duck Harbor have significantly more seedling emergence than High Head.

All sand dune communities are subject to disturbances that result in movement of sand. Our initial intent was to compare the seed banks of sand dunes with histories of intense anthropogenic disturbance with "undisturbed" dunes that were not subject to anthropogenic disturbance. However, natural and anthropogenic disturbance may both have important consequences for sand dune seed banks. Increased aeolian sand transport enhanced by anthropogenic disturbance of sand stabilizing vegetation (High Head) may cause permanent removal of seeds carried with eroding sand. Natural overwash (Coast Guard) may also effectively remove seeds from the seed bank by burying them too deeply for germination to occur. Either process would result in a depauperate seed bank and would provide similar results in a study such as ours. A second goal of this study was to assess the potential for existing seed banks to restore species diversity to degraded dunes replanted with *Ammophila breviligulata* and the feasibility of using sand imported from other dunes for this purpose. The results indicate that sand dune seed banks have low species diversity and low seed densities and therefore are not likely to be useful additions for restoration efforts aimed at increasing sand dune species diversity.

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NEW ENGLAND NOTE

BARNSTABLE COUNTY RECORDS FOR *SCLERIA PAUCIFLORA* VAR. *CAROLINIANA* AND *POTAMOGETON AMPLIFOLIUS*

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About 25 specimens of *Scleria pauciflora* Muhl. var. *caroliniana* (Willd.) Wood (Cyperaceae) were observed on July 26, 1997 while conducting an inventory of the *Malaxis bayardii* Fern. population at a sandplain grassland field in Forestdale, Massachusetts. Previously verified reports for *S. pauciflora* have been restricted to Martha's Vineyard and Nantucket Island, with one early report from a public golf course in Barnstable, Massachusetts (LeBlond 1988). This species is listed as Endangered (S-1) in Massachusetts.

Sorrie and Dunwiddie (1996) describe the plant as very rare in the sandplain grasslands at Ram Pasture and Trotts' Hills on Nantucket. This variety is characterized by having a pilose culm and leaves, rather than being glabrous as in var. *pauciflora*. Carolina-whipgrass ranges from southwestern New Hampshire south to Florida and Texas and inland to Michigan and Missouri. This record documents the second Barnstable County occurrence for this species.

The Forestdale plants were observed in the open scrub-pitch pine ecotone bordering a sandplain grassland community established on a seven acre open field. The field is mowed periodically during the growing season for recreational use. Associated taxa in the field edge habitat included several uncommon to rare species such as *Aletris farinosa* L., *Linum intercursum* E. Bickn., *Linum virginianum* L., *Bartonia virginica* (L.) BSP., *Lycopodium clavatum* L., *Lespedeza angustifolia* (Pursh) Elliott, and *Polygala nuttallii* T. & G. During the field visit, 120 *Malaxis bayardii* plants in full anthesis were recorded, making this the largest recorded population in Massachusetts (P. Somers, pers. comm.).

While conducting an inventory of the aquatic macrophytes in Red Brook Pond in Pocasset, Massachusetts, the authors collected a specimen of *Potamogeton amplifolius* Tuckerman (Potamogetonaceae). Although common elsewhere in the state, this appears to be the first record of this distinctive species for the Cape and Islands (Hellquist and Crow 1980). Several submerged specimens were observed and collected on September 10, 1997 in relatively shallow (1–1.5 m) water in the western section of Red Brook Pond. This species generally prefers neutral to basic pH levels rather than the usual acidic waters of the Cape (Hellquist and Crow 1980). Submerged leaves were large (>20 cm) and falcately folded with distinct venation and stipules. Floating leaves and flower stalks were not observed, though the absence of floating leaves is not uncommon (Hellquist and Crow 1980).

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BOOK REVIEW

The Illustrated Companion to Gleason and Cronquist's Manual: Illustrations of the Vascular Plants of Northeastern United States and Adjacent Canada by Noel H. Holmgren. 1998. xvi + 937 pp. line drawings. ISBN 0-89327-399-6 $125.00 (hardback). The New York Botanical Garden, Bronx, NY.

One of the most difficult tasks in teaching plant identification is that of helping students become comfortable with technical keys and descriptions. All too often I find students resorting to their field guides, with alluring color photos or line drawings and no difficult or confusing terminology. I rejoiced when the second edition of Gleason and Cronquist's *Manual of Vascular Plants of Northeastern United States and Adjacent Canada* was published in 1991. Although many students (like myself 20 years ago) still whine their way up that steep slope to the plateau of accomplishment, I find most students eventually have a high degree of success in keying the local flora without much interference from me.

My new class stumbling block is that the students still would like a visual confirmation of their identification in some cases. Back to the field guides, with the main disadvantages being that all of our local flora isn't illustrated, and that, in many cases, students still aren't able to distinguish between similar species. I sometimes borrow our herbarium library's volumes of Gleason's 1952 *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada* for class use, but I find students reluctant to use these because of the outdated nomenclature. If students are feeling overwhelmed using one technical manual they are unlikely to subject themselves to a second with new and different idiosyncracies. Likewise, they rarely explore the herbarium to confirm or reject an identification.

Thus, I was very happy to receive the newly published *The Illustrated Companion to Gleason and Cronquist's Manual.* Noel Holmgren, with the artistic and editorial assistance of Patricia K. Holmgren, Robin A. Jess, Kathleen M. McCauley, and Laura Vogel, has compiled a volume of illustrations that combines the taxonomy in Gleason and Cronquist's second edition with the high quality illustrations in Gleason's *Illustrated Flora.* But the new volume is not merely a rearrangement of the old illustrations; new drawings were made for species described since 1952, new details were added to some illustrations, and a reassessment of diagnostic features was made where species have been placed in synonymy or names misapplied. The result is a volume of accurate technical illustrations with updated taxonomy corresponding to the best volume of technical keys and descriptions for the northeastern United States and adjacent Canada. My students will be ecstatic!

Beyond the classroom, this volume should appeal to professionals, too. Many of us have suffered the frustration of trying to identify a difficult unknown without herbarium specimens for comparison. Also, good technical illustrations can help us where herbarium specimens sometimes cannot, like with dissections of flowers or fruits. I always feel much more confident with the identification of an unknown grass if I have Gleason's *Illustrated Flora* close by!

The Illustrated Companion to Gleason and Cronquist's Manual probably will be most useful in the lab. Its weight (6 lb. on my bathroom scale) and 8 × 11 inch size will preclude use as a field guide. Since the drawings have been made from herbarium specimens, the "match" for some specimens will be best when they are flat, too.

The book has some useful and interesting features beyond the illustrations, as well. In the introduction, the author details the histories of Gleason's *Illustrated Flora* and Gleason and Cronquist's *Manual*, and he describes how they come together in this new book. There is also information provided on the artists whose anonymous contributions graced the *Illustrated Flora*. Since the taxonomy of our flora is ever-changing and many of the names used in Gleason and Cronquist's second edition are already outdated, the *Illustrated Companion* has an appendix cross-referencing names used in Gleason and Cronquist's second edition (and, thus, this new book) with those used in *Flora of North America, Volume 2* and *Volume 3*. The book has two indexes. The first is an index to all common names used in Gleason and Cronquist's second edition, and includes the scientific name for each entry in parentheses for convenience. The second is an index to scientific names.

Overall, *The Illustrated Companion to Gleason and Cronquist's Manual* will be a much-appreciated addition to our class, herbarium, and personal libraries. It will be an indispensable tool to students and professionals identifying vascular plants in the northeastern United States and adjacent Canada.

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—JANET R. SULLIVAN, Department of Plant Biology, University of New Hampshire, Durham, NH 03824.

RHODORA, Vol. 100, No. 903, pp. 319–321, 1998

BOOK REVIEW

Intermountain Flora: Vascular Plants of the Intermountain West, U.S.A.: Volume Three, Part A: Subclass Rosidae (except Fabales), by Arthur Cronquist, Noel H. Holmgren and Patricia K. Holmgren. 1997. 446 pp. ISBN 0-89327-375-9 $75 (hardback). The New York Botanical Garden, Bronx, NY.

This is the penultimate work in a seven volume *magnus opus* for the plants of the intermountain west, an area of the western United States which includes all of Utah, most of Nevada, and parts of Arizona, California, Idaho, and Oregon. Twenty-five years in the making, its completion has been long awaited by ecologists and the botanical community. This volume treats all of the Rosidae with the exception of the Fabales (published separately as part B, and authored by Rupert Barneby), and for the first time, provides a synthetic treatment of some of the most complex families in the region.

The intermountain region has been one of the last frontiers for botanical exploration in North America. It is an area where scores of new species have been discovered in the past two decades and frequent range extensions are recorded. The completion of the *Intermountain Flora* will stimulate systematic research in this highly dissected, remote, and rapidly changing landscape.

For the first time in the publication of the series, there is a byline attributing authorship for each family—a convention which is enormously helpful in assigning responsibility for the taxonomic treatments. Arthur Cronquist, the first author of this volume, was working actively on treatments when he died in 1992. Much of his work was in draft form and in need of considerable editing; my sense of the situation is that Noel Holmgren and Patricia Holmgren did not add their names as authors unless they made extensive revisions. Of the 40 families treated in the work, authorship (indicated in parentheses) is fairly evenly divided and treatments of some problematic groups are especially welcome: Apiaceae (AC), Rosaceae (NHH), Onagraceae (AC, NHH, PKH), and Grossulariaceae (PKH).

While this work is important in a number of ways, its chief significance lies in the fact that few regional floras rival the *Intermountain Flora* in scope or detail. Previous volumes have been used as a standard against which other floristic works are judged, and the present volume is no exception. Following the format used in the first five volumes, Noel Holmgren and Patricia Holmgren made a welcome addition to the standard format by treating commonly cultivated horticultural taxa in the keys. As with the standard format, all native and naturalized taxa are accompanied by lengthy morphological descriptions, illustrations, and full taxonomic and nomenclatural synonymy which includes bibliographic citations and type specimen information for all basionyms. Descriptions of habitat and distribution are often accompanied by a discussion of morphological variation by geographic region and the ensuing problems with taxonomic circumscription. References to dissenting points of view are usually provided, and the authors spare no effort in offering lengthy discussions about problematic species and species complexes. The text of the *Intermountain Flora* is rich with personal field observations providing details found in no other reference. Decades of experience are distilled in the volumes and the treatments show a zealous attention to detail. Users of the flora will be delighted by the clearly written keys, lively discussions, and lavish illustrations.

While anyone working with the treatments might disagree with some of the circumscriptions of taxa in the flora, no one can fault either the quality of the work and the precision of the keys, or fail to enjoy the lively discussions. Lavish illustrations make the work enormously useful, enhancing its value as a scientific document and greatly enhancing its popularity with the general public. The appreciation by the authors is shown in their dedication to artists Jeanne R. Janish, Bobbi Angell, and Robin Jess, "whose skillful drawings give vivid life to the text."

My only criticisms of this volume are the omission of an introduction providing background information on the flora, the absence of a bibliography of previous volumes, and no mention of the final volume (number two), which will include a key to families. During my fifteen years as the curator of the Intermountain Herbarium, the question I was asked most frequently was "When will the next volume of the Intermountain Flora be published?" Now, the question will be "When will a synoptic volume be published?" Knowing that the Holmgrens will complete this work in the near future, we in the systematic community owe them our gratitude and hearty congratulations.

—Leila M. Shultz, Harvard University Herbaria, Cambridge, MA 02138, and the Floristics Laboratory of Utah State University, Logan, UT 84322-5215.

RHODORA, Vol. 100, No. 903, pp. 322–328, 1998

NEBC MEETING NEWS

April 1998. Dr. John Beaman, the Club's Distinguished Speaker for 1998, was given a long introduction by former student, Dr. Garrett Crow. In 1983–84, Dr. Beaman held a Fulbright Fellowship, which enabled him to initiate his study of the flora of Borneo's Mount Kinabalu, which he has continued ever since, but particularly from 1994 to 1996 during two years as founding director of the Institute of Biodiversity and Environmental Conservation of University Malaysia Sarawak, and since then as an Honorary Research Fellow at The Royal Botanic Gardens, Kew, England.

John Beaman began by acknowledging that he could not feel too smug in being the Distinguished Speaker, given that it had been 44 years since his first and only other presentation to the Club. He then launched into his lecture entitled "The Systematics and Evolution of the Flora of Mt. Kinabalu (Borneo): An Example of Conservation Biology in Action." Via spectacular images, we were quickly taken to a lushly vegetated mountain with precipitous slopes and waterfalls located a few degrees north of the equator in northern Borneo, where Beaman, his son Reed (named for Dr. Reed Rollins), and about 40 other collaborators have been engaged in a number of projects aimed primarily at achieving a better understanding of the evolutionary and phytogeographic significance of the mountain and its flora. Part of Kinabalu's significance is that it is the highest mountain (c. 4100 m) between the Himalayas and the mountains of New Guinea. We were given a quick tour up the mountain through five elevationally defined zones: 1) lowlands with rattans (viny, spiny palms), some over 150 ft. long; 2) hill forests with the world's largest orchid, *Grammatophyllum speciosum,* growing epiphytically; 3) lower montane forest—the zone with the most species-rich elevation on the mountain at about 1500 m, and taxa including *Viburnum* and many orchids; 4) upper montane forest—a zone with three species of gymnosperms belonging to the Phyllocladaceae and Podocarpaceae. The celery pine *Phyllocladus hypophyllus* has false leaves, actually flattened stem tissue, anatomically. Isozyme studies of the genus *Leptospermum* from this elevation suggest that one of the species, now a dominant in an elfin forest community at 3000 m, has a post Pleistocene origin; 5) an open granitic summit with glacial scars from 9500 yrs. BP and interesting plants in its crevices and seeps. Interestingly, GIS studies relating floristic diversity to unit area revealed that species per 10 km^2 was actually greatest at 2500–3000 m, rather than at lower elevations.

Kinabalu is a batholith of granite formed in the Pliocene (c. 1–2 million years BP) under water, then uplifted in the Pleistocene through sedimentary formations. Because the mountain is young geologically and has a history of glaciation, Beaman and colleagues found it to be an ideal outdoor lab for studying examples of rapidly evolving plant groups. Ultramafic areas of serpentine at mid- and lower elevations have especially rich floras. Genetic studies of tree fern taxa on Kinabalu by Dave Conant, for instance, showed an endemic to the serpentine with likely derivation from a species in an adjacent geological formation. Studies of *Dendrochilum, Polyosma, Cyathea, Lithocarpus, Carex,* and *Rhododendron* are among those receiving the attention of collaborating systematists currently.

The flora has proven to be one of the most diverse in the world. There are many genera rich in species, including the figs with about 100 taxa. One ultramafic serpentine area of hardly more than 100 ha has over 300 species of orchids. One of Beaman's projects has involved the employment of local people in documenting the flora. This has been very successful and has significantly expanded the number of species, especially in certain groups like the palms, where extra money was paid per specimen collected. The botanical inventory has resulted in two books thus far. One covers the pteridophyte flora with 620 species, ⅓ more taxa than on the entire African continent; the other enumerates 711 orchid taxa. His most recent and still unpublished work is an enumeration of the gymnosperms and non-orchid monocotyledons. Using the Cyperaceae as an exemplar group he illustrated that the closest floristic affinities are with continental Asia, but that other taxa are of Malesian and Australian affinity. The mountain has many neo-endemics, suggesting that a very rapid evolutionary process is happening on the mountain. Among the most interesting endemics are some of the pitcher plants, *Nepenthes,* with several species restricted to serpentine. He also showed a common lowland species with vestigial pitcher lids. The endemic *N. rajah* has the largest pitchers in the genus, and has even been known to trap mice.

Macrophotography through the base of the giant flowers of

Rafflesia pricei, in the genus with the largest known flowers, illustrated what Beaman and his students have learned about its pollination ecology. The flowers are unisexual and pollinated by carrion flies, which are guided by the odor and appearance of rotting meat to anthers on male flowers, where they are precisely positioned by internal bristly ridges to pick up a load of pollen on their backs. When they go to a female flower the pollen load is rubbed off on the broad stigmatic surface of the female flowers. The Beaman team has hypothesized that the flies are deceived into visiting *Rafflesia* flowers as potential brood places. They receive no reward for their efforts, however. A slide was used to illustrate one site of this important study area that has since been lost to slash and burn practices.

Unfortunately, Kinabalu, like so many other tropical areas, is under siege. Slash and burn agriculture, copper and gold mining, and illegal logging within park boundaries have had major impacts. Some areas once species-rich have been cut and burned, and Beaman believes they will never recover lost species and ecosystem characteristics. Much responsibility rests on the shoulders of Malaysian botanists and naturalists who are studying and attempting to educate others about their rich and endangered flora. In response to questions after the talk, it was pointed out that the biologists and park managers are working very hard to preserve their precious natural resources.

For additional reading about Mount Kinabalu, Dr. Beaman recommends a book on the natural history of the mountain published in 1996, entitled *Kinabalu—Summit of Borneo,* edited by K. M. Wong and A. Phillipps and published by the Sabah Society.

—PAUL SOMERS, Recording Secretary.

May 1998 Field Trip. Fifteen Club members and families enjoyed an unseasonably warm hike up Mt. Major on Alton Bay, NH, on May 1st to search for early spring blooms. The trail led up through dry hemlock/beech/oak/red maple woods with *Acer pensylvanicum, Viburnum alnifolium, Uvularia sessilifolia, Viola fimbriatula, Diervilla lonicera, Prunus pensylvanica, Vaccinium angustifolium* and several tantalizing carices in bloom. The higher rocky outcrops below the 1784-foot summit yielded *Epigaea repens, Amelanchier bartramiana,* and *Arctostaphylos uva-ursi* in bloom, as well as *Clintonia borealis* in bud and spectacular views of Lake Winnipesaukee. The group also observed the remarkable and extensive tree damage from the winter ice storms.

—Lisa A. Standley

May 1998. Dr. Garrett Crow from the University of New Hampshire spoke on the topic "Biodiversity of Aquatic Plants in Costa Rica and Bolivia: Is New England Really the Amazonia of Aquatic Diversity?" Utilizing floristic data from his aquatic plant research in Costa Rica, which began in 1984 with a sabbatical at the Universidad Nacional de Costa Rica, and recent trips to Bolivia to assist doctoral student, Nur Ritter, Garrett attempted to convince us that northern temperate aquatic ecosystems in formerly glaciated New England and Michigan were often equal to or more species-rich than those of comparable size and general ecological character at his tropical sites. This, of course, is contrary to the general pattern where vascular plant floras in tropical areas are dramatically larger than their temperate counterparts of comparable size. Demonstrating this general trend, he stated that Costa Rica has a very rich flora comprised of 10–12,000 vascular plant species, whereas the Carolinas, which are over four times larger, have only 3360 species. His inventories of wetlands in Costa Rica and Bolivia often showed the opposite pattern, with fewer or comparable numbers to those found at New England sites studied by himself and others.

To better understand this apparent reversal of the normal phenomenon, he looked at the problem from two approaches: 1) by comparing species richness latitudinally on a similar habitat basis, and 2) by comparing richness in various taxonomic groups among regional aquatic plant floras. Many examples of the habitat basis comparisons were given. The individual floras of two ponds in Puntarenas, C.R., were comparable in number, about 20 species, to that of Turtle Pond in Lee, N.H., but the flora of Costa Rica's Lago Hule was only 25 species compared with the 125 species reported by Hellquist for New Hampshire's Lake Ossipee. Also, peatlands of New Hampshire and Michigan, when compared to páramo and sphagnum bogs of Costa Rica's Cordillera de Talamanca, came up much higher in species' numbers. In defense of the páramos, however, he noted such interesting species as *Puya dasylirioides,* a spectacular bromeliad, and *Drimys granadensis* in the Winteraceae, a primitive angiosperm family. Applying his second approach, he compared numbers of species in aquatic plant families in three regions: northeastern North America, southeastern United States, and Central America. The total number of species (145) was slightly higher in the northeastern U.S. than in the southeastern U.S. (122 spp.) or Central America (120 spp.). Comparing individual families across the three regions, he showed that certain families, e.g., Eriocaulaceae and Mayacaceae, had the most taxa in Central America, but many other groups, such as the Cyperaceae and Haloragaceae were highest in the northeastern U.S. and poorly represented in Central America.

Garrett then took us south to Bolivia where he and Nur Ritter have been further examining aquatic plant diversity. Bolivia is approximately two times the size of Central America. It is much less explored than Central America botanically (1/10th the number of collections), but is estimated to have a flora of 18,000 vascular plant species. Starting in the Cochabamba Valley, our northern botanists headed off to explore wetlands ranging from a sphagnum bog at 2920 m elevation with 21 species to some tropical lowland sites in the upper Amazon Basin where some of the highest species counts (65–84 species) were obtained. While many interesting and beautiful species were observed, the species richness was generally equal to or less than in the northeastern U.S.

It is Garrett's hope that his investigations will help conservationists set priorities regarding protection of wetland habitats. In Costa Rica's Palo Verde/Rio Tempisque, for instance, where 97 species occur, this should be valued as an area of high tropical diversity, even though lower than that found in many temperate swamplands. He also hopes that these studies will further the recognition of northern temperate wetlands of New England as the "Amazonia" of aquatic diversity. When asked afterwards why he thought diversity was higher in the northeastern U.S., he speculated that there appears to be a relationship between high diversity and areas glaciated during the Pleistocene. As support for this he noted the relatively low diversity in unglaciated areas of Siberia.

June 1998. Dr. Aaron M. Ellison, Fisher Associate Professor of Environmental Studies in the Department of Biological Sciences at Mount Holyoke College, addressed the topic "Direct Interactions Between Northern Pitcher-plants (*Sarracenia purpurea*) and

Their Associated Animal Communities." His talk dealt with research ideas being explored by himself, students, and Nicholas J. Gotelli, a collaborator at the University of Vermont.

The Sarraceniaceae, or pitcher-plant family, occurs only in the western hemisphere. Members of the family in the genera *Sarracenia, Darlingtonia,* and *Heliamphora* are characterized by pitcher-like leaves that trap water and in it a variety of organisms. How are these pitchers formed? What environmental and physiological factors influence the formation of pitchers? These are among the questions for which the researchers are seeking answers. Using a two hectare sphagnum bog mat at Hawley Bog in Franklin County, Massachusetts, as an outdoor research area and with more controlled environments provided by greenhouses, the researchers will attempt to quantify energy and nutrient inputs and outputs from purple pitcher-plants, *S. purpurea,* in order to better understand the factors influencing pitcher formation. These results may be applicable to the eastern hemisphere pitcher-plant families Nepenthaceae and Cephalotaceae.

Ellison presented several perspectives on pitcher-plant ecology. From an insect's perspective, pitchers are distributed in a patchy fashion and are of various quality for meeting their needs. The insects themselves play an important role in controlling the quality of these patches. A typical zoologist's view of pitcher-plants, he said, is to treat them as vaselike organisms containing an aquatic ecosystem. Their studies thus far have involved examination of the relationships among protozoans, mosquitoes, flies, rotifers, midges, mites, yeast, and bacteria. In a given year, pitcher leaves are colonized by three basic communities of organisms: one dominated by rotifers and mites, one dominated by midge and mosquito larvae, and one consisting only of larvae of a sarcophagid fly. Rotifers such as *Habrotrocha rosa,* via their excretion rates, may be capable of supplying all the pitcher-plants' needs for nitrates, ammonia, and phosphate. The quality of the pitcher-plant patches varies, he said, depending in large part on what the inhabitants do. The botanical view focuses mainly on the "living plant" and takes into consideration the role of photosynthesis, growth rates, and how these factors and nutrients influence pitcher leaf formation and flower production. Is there any relationship between pitcher nutrients and growth? One research question being asked is whether or not adding nutrients to the pitchers will influence leaf production. In the oligotrophic bog environment, it has been assumed that few nutrients are taken up by the roots even though they may be well developed. Ellison's goal is to get the complete "pitcher," relating both botanical and zoological aspects to how pitcher plants function.

Part of getting the complete "pitcher" has involved monitoring the Hawley Bog population. Monitoring in 1996 and 1997 has shown there is considerable year to year variation in the percent that produce flowers (ca. 10% in '96 vs ca. 50% in '97) and in the number of pitcher vs. flat leaves (called phyllodia) produced. Interestingly, the phyllodia, which are also referred to as winter leaves, sometimes produce rudimentary pitchers at their apices. What factors determine flower or pitcher production? Why should plants produce pitchers at all, Ellison has asked? Since flat leaves intercept more light, they may be more effective at delivering the benefits of photosynthesis. Why be carnivorous? Since bogs are high light but low nutrient environments, a role in providing key nutrients is generally regarded as a reason for carnivory. By carefully monitoring and modeling the nutrient conditions in the bog habitat, in the pitcher-plants, and in the pitchers with their inquiline assemblages, Ellison and company hope to better understand the complexity of these interrelationships and what triggers the pathway to carnivory.

—PAUL SOMERS, Recording Secretary.

ANNOUNCEMENT

NEW ENGLAND BOTANICAL CLUB GRADUATE STUDENT RESEARCH AWARD

The New England Botanical Club will offer $2,000 in support of botanical research to be conducted by graduate students in 1999. This award is made annually to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so.

The award will be given to the graduate student(s) submitting the best research proposal dealing with systematic botany, biosystematics, plant ecology, or plant conservation biology. It is anticipated that two awards will be given, although the actual number and amount of awards will depend on the proposals received.

Applicants must submit a proposal of no more than three double-spaced pages, a budget, a curriculum vitae, and two letters in support of the proposed research, one from the student's thesis advisor. Three paper copies of the proposal, budget, and CV must be submitted.

Proposals and supporting letters must be received no later than March 1, 1999. The recipient(s) will be notified by April 30, 1999. Send proposals to: Awards Committee, The New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138.

Two Graduate Student Research Awards were given in 1998. Ms. Sonja Schmitz of the University of Vermont received support for her proposal entitled "Inferring evolutionary and biogeographic history from patterns of genetic variation in inland and coastal beachpea (*Lathyrus japonicus*) populations." Mr. David Moeller of Cornell University received support for his proposal entitled "The ecology and evolution of self-pollination in Blue Flag, *Iris versicolor:* An island-mainland comparison."

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ABSTRACT: An abstract and a list of key words should be included with each paper, except for shorter papers submitted as Notes. An abstract must be one paragraph, and should not include literature citations or taxonomic authorities. Please be concise, while including information about the paper's intent, materials and methods, results, and significance of findings.

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FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad

distribution. Keys and synonymy for systematic revisions should be prepared in the style of "A Monograph of the Genus *Malvastrum*," S. R. Hill, RHODORA 84: 159–264, 1982. Designation of a new taxon should carry a Latin diagnosis (rather than a full Latin description), which sets forth succinctly how the new taxon differs from its congeners.

LITERATURE CITED: All bibliographic entries must be cited in the paper, unless a special exception has been made by the Editor (such papers will be allowed a REFERENCES section). Verify all entries against original sources, paying special attention to spelling and details of publication. Cite references in strict alphabetical order by first author's surname. Do not write authors' names in all capital letters. References by a single author precede multi-authored works of same senior author, regardless of date. Use a long dash when the author(s) is the same as in the entry immediately preceding (see recent issues). Refer to Botanico-Periodicum-Huntianum (B-P-H 1968) and B-P-H/Supplement (1991) for standardized abbreviations for journals.

TABLES: Tables must be double-spaced. Tables may be continued on an extra page, if necessary. As much as possible, the title should be self-explanatory. Do not use footnotes; instead, add notes after the end of the table title. Broadside tables should be avoided, if possible. Each table should be cited in the text in numerical order.

FIGURES: Illustrations must be either black and white half-tones (photographs), drawings, or graphs. Illustrations must be camera-ready; flaws cannot be corrected by the Editor or the printer. Add symbols or shading with press-on sheets. The printed plate will be 4 × 6 inches; be sure that illustrations are proportioned to reduce correctly. Allow space for a caption, if possible. Magnification/reduction values should be calculated to reflect the actual printed size. Maps must indicate scale and compass direction. The double-spaced list of legends for figures should be provided on a separate page. Each figure should be cited in the text in numerical order.

THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
Cambridge, MA 02138

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FLORISTIC AND ZONATION STUDIES OF SEAWEEDS FROM MOUNT DESERT ISLAND, MAINE: AN HISTORICAL COMPARISON

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ABSTRACT. Based upon recent collections at 28 sites plus historical data from the last century, the macroalgal flora of Mount Desert Island consists of 41 Chlorophyceae, 50 Phaeophyceae, and 55 Rhodophyceae. Previously, 121 seaweeds were recorded from Mount Desert Island and 113 taxa were found during present sampling. A comparison of the two time periods shows 88 taxa in common or a 75% similarity. Varying percent similarity patterns are evident when historical and present collections at Otter Cliffs (68%), Seal Harbor (43%), and the Seawall-Southwest Harbor areas (54%) are compared. The reduced values for Seal Harbor may reflect anthropogenic effects, while the other values may represent varying levels of taxonomic characterization and/or temporal variability of floras. Pronounced habitat diversity on Mount Desert Island probably causes the relatively low intra-island similarity patterns ($\bar{x} = 36.8 \pm 7.6\%$), while interisland comparisons of other Northwest Atlantic islands are much higher (ca. 51.0–92.0%, $\bar{x} = 72.3\% \pm 6.0\%$). In comparing species richness around Mount Desert Island, the largest numbers of taxa occur on the exposed coasts at Otter Cliffs and Seawall that experience intense wave activity, while the lowest numbers occur at several sheltered sites.

Zonation patterns at three representative sites (exposed Otter Cliffs, protected Otter Cove, and sheltered Thompson Island) show pronounced localized differences. The biological zones at Otter Cliffs exceed mean tidal amplitude, and patterns of species richness there are also higher than at the other two Mount Desert sites. Green algae show the most conspicuous decrease in species richness with increasing shelter. Of the 32 intertidal species in common with a 1928 zonation study at Otter Cliffs, 13 showed a conspicuous reduction in their upper distributional limits (0.5 to 2.0 m), while none showed an upward expansion. Such reductional patterns may reflect either a general warming trend in the Gulf of Maine or the effects of air pollution during intertidal exposure.

Key Words: seaweeds, history, ecology, Mount Desert Island, Maine, Gulf of Maine

Mount Desert Island, which is the largest insular habitat (Figure 1, 2) on Maine's extensive and indented coastline (Platt 1996; Simpson 1987), has a long and unique phycological history. Rand and Redfield (1894) produced an initial catalogue of its plants (phanerogamic and cryptogamic), as well as a synopsis of the island's ecology, geology, and postglacial history based upon studies initiated during the early 1880s. Two noted phycologists, Frank Shipley Collins and Isaac Holden, studied the algae, recording approximately 100 taxa from the exposed, eastern shoreline and nearby Cranberry Isles (Collins 1894). Several other new taxa were recorded in *Phycotheca Boreali-Americana*, the largest exsiccata of seaweeds ever published (cf. Setchell 1925; Taylor 1957). Taylor (1921) listed a few additional seaweeds based upon summer collections during 1915 and 1920. Johnson and Skutch (1928a, b, c) described the species composition, zonation, and ecology of intertidal algae at Otter Cliffs, an exposed promontory on the eastern side of the island (site 11; Figure 2, 3A). It is still one of the most significant studies of its kind for any part of the Maine coastline (Mathieson et al. 1991).

In the present study, the floristic composition and zonation of seaweeds from Mount Desert Island, Maine, are described utilizing recent and historical collections from the last century plus detailed zonation comparisons at Otter Cliffs (Johnson and Skutch 1928a, b, c). The seaweed zonation is also compared with recent studies at Bald Head Cliff, York, Maine (Femino and Mathieson 1980), and Jaffrey Point, Newcastle, New Hampshire (Mathieson et al. 1981). As noted by Barry et al. (1995), the diverse impacts of man on coastal resources are often difficult (impossible) to assess because few detailed "baselines" exist for comparisons. With Mount Desert's long phycological history and the fact that it now contains one of the most popular national parks in the United States (Acadia), such comparisons can be used to assess shifts in the macroalgal communities in the future. The specific objectives of our field studies are fourfold: (1) to assess the number and types of seaweeds at diverse sites around the island; (2) to compare present and previously documented patterns of species richness and composition at three sites; (3) to compare present patterns of zonation among three Mount Desert sites, as well as two others in southern Maine and New Hampshire with variable wave exposure; and (4) to compare present and previous patterns of seaweed zonation at Otter Cliffs, Bar Harbor.

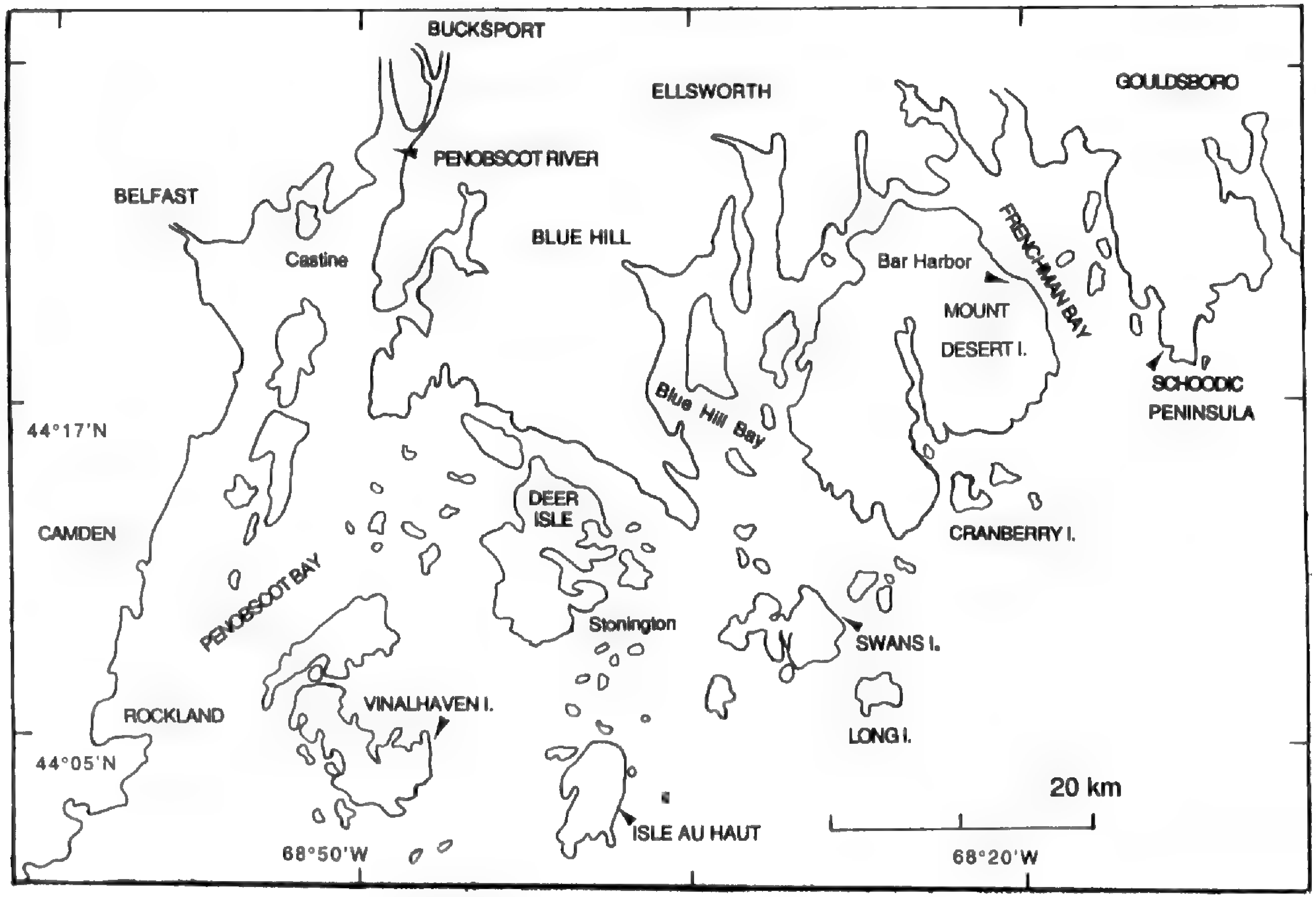

Figure 1. Mid-coastal Maine between Rockland (Penobscot Bay) and the Schoodic Peninsula, including Mount Desert Island.

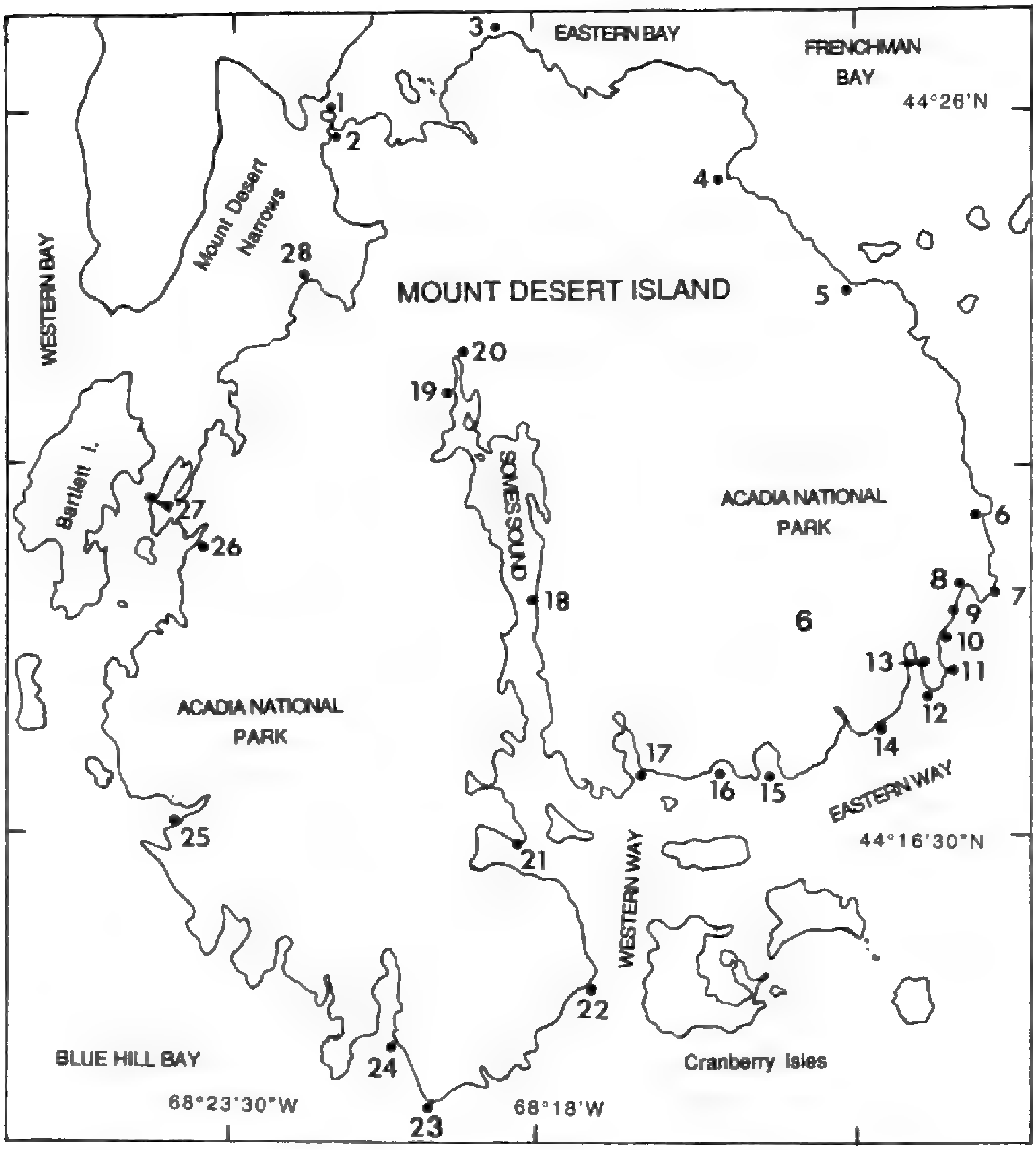

Figure 2. Mount Desert Island showing the location of 28 recent collecting sites.

MATERIALS AND METHODS

Floristic studies. In assessing present floristic patterns on Mount Desert Island, extensive year-round collections and observations of intertidal and shallow subtidal seaweeds were made at 28 locations (Figure 2; Table 1; Appendix). The sites were established clockwise around the island, starting at Thompson Island on Mount Desert Narrows (site #1) and ending at Indian Point on Western Bay (site #28). Old House Cove (#2) and Indian Point (#28) are closest to Thompson Island. Four primary considerations were important in establishing these study sites: (1) acces-

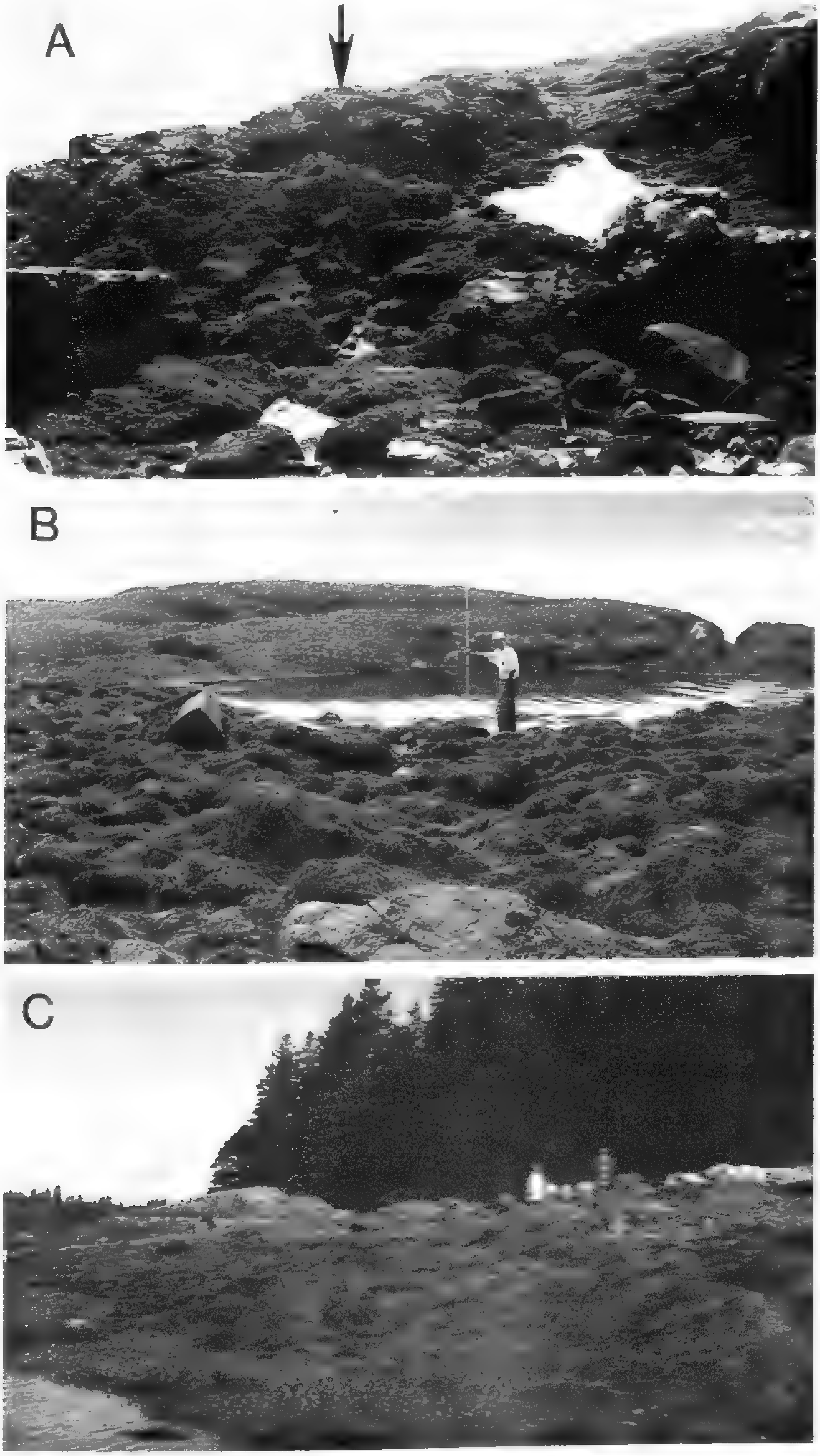

Figure 3. Three Mount Desert habitats where zonation studies were conducted during 1996. (A) Otter Cliffs: an exposed site showing Johnson and Skutch's (1928a) bench mark (arrow) plus a large tide pool. (B) Otter Cove: a sheltered site with a dense growth of fucoid algae. CJD is holding a stadia rod near the extreme lower intertidal region. (C) Thompson Island: a protected habitat with scattered boulders, abundant *Ascophyllum nodosum*, a fringing *Spartina* salt marsh (ACM standing), and contiguous terrestrial vegetation.

Table 1. Historical and recent collections from Mount Desert Island and adjacent Cranberry Isles, plus percent occurrence at twenty-eight present-day sites. See Appendix for numerical site designation, plus dates of collections and collectors; X = recorded by Collins (1894) as being common but no specific locations given.

	Historical Collections	Present Collections (% Occurrence)
BACILLARIOPHYCEAE		
Berkeleya rutilans (Trentopohl) Grünow		3, 6–8, 10–13, 15–17, 22, 23, 26 (50%)
TOTAL DIATOM TAXA	0	1
COMBINED TOTAL DIATOM TAXA (1)		
CHLOROPHYCEAE		
Blidingia minima (Nägeli ex Kützing) Kylin	11, 15, 21	6, 7, 11, 13, 14, 16, 17 (25%)
Bolbocoleon piliferum N. Pringsheim	15	(0%)
Capsosiphon fulvescens (C. Agardh) Setchell et N. L. Gardner	15, 16	6, 12, 19, 20 (11%)
Capsosiphon groenlandicum (J. Agardh) K. L. Vinogradova	14a	10 (4%)
Chaetomorpha aerea (Dillwyn) Kützing	17a	14 (4%)
Chaetomorpha brachygona Harvey		14 (4%)
Chaetomorpha linum (O. F. Müller) Kützing		2, 15, 22, 26 (11%)
Chaetomorpha melagonium (Weber et D. Mohr) Kützing	11, 17a, 21, 22	6, 7, 10, 11, 14, 22 (21%)
Chaetomorpha picquotiana Montagne ex Kützing		2, 15, 17 (11%)
Chlorochytrium schmitzii Rosenvinge	15	(0%)
Cladophora rupestris (L.) Kützing	22	(0%)
Cladophora sericea (Hudson) Kützing	11, 15, 17a, 21, 22	7, 9, 11–14, 21, 24, 26 (32%)
Cladophora vagabunda (L.) C. Hoek	16, 17a, 21	(0%)
"*Codiolum petrocelidis* Kuckuck"	14a, 15	14, 22, 23 (11%)
"*Codiolum pusillum* (Lyngbye) Kjellman"	11, 15, 22	11–13, 22 (14%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Enteromorpha clathrata (Roth) Greville	15, 16	6, 7, 12, 14, 22 (18%)
Enteromorpha compressa (L.) Nees	11, 15, 21	13 (4%)
Enteromorpha flexuosa (Wulfen ex Roth) J. Agardh ssp. *paradoxa* (Dillwyn) Bliding	15, 17a	(0%)
Enteromorpha intestinalis (L.) Nees	15, 21	5–16, 19, 22, 23 (54%)
Enteromorpha linza (L.) J. Agardh	15	5, 10, 11 (11%)
Enteromorpha prolifera (O. F. Müller) J. Agardh	17a	11, 12, 24 (11%)
Enteromorpha torta (Mertens in Juerg.) Reinbold		20, 26 (7%)
Epicladia flustrae Reinke		13, 23 (7%)
"*Gomontia polyrhiza* (Lagerheim) Bornet et Flahault"	15	(0%)
Microspora pachyderma (Wille) Lagerheim		7, 12, 16, 17, 20–22, 26, 28 (32%)
Monostroma grevillei (Thuret) Wittrock	11, 17a	3–8, 10, 12, 14–18, 22, 23, 25, 26, 28 (61%)
Percursaria percursa (C. Agardh) Bory	15, 21, X	2, 21, 26 (11%)
Pilinia endophytica Collins		3, 15 (7%)
Prasiola stipitata Suhr in Jessen		11 (4%)
Protomonostroma undulatum (Wittrock) K. L. Vinogradova f. *pulchrum* (Farlow) M. Wynne	22	5, 8, 10, 12, 14, 16, 22 (25%)
Rhizoclonium riparium (Roth) Kützing ex Harvey	15, 21	2, 4, 16, 17, 20, 24, 26, 28 (29%)
Rhizoclonium tortuosum (Dillwyn) Kützing	11, 21a	5, 6, 10–14, 22 (29%)
Spongomorpha aeruginosa (L.) C. Hoek	14a, 15, 17a	(0%)
Spongomorpha arcta (Dillwyn) Kützing	11, 15, 21, 21a, 22	5–15, 22 (43%)
Spongomorpha spinescens Kützing	11, 15, 21, 22	11, 21 (8%)
Ulothrix flacca (Dillwyn) Thuret in Le Jolis	11, 13a	(0%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Ulothrix speciosa (Carmichael ex Harvey in Hooker) Kützing		5, 7, 10, 16, 17, 21 (21%)
Ulva lactuca L.	11, 15	4–8, 10–17, 22 (46%)
Ulvaria obscura (Kützing) Gayral	15	6, 10–15, 19, 22, 23 (36%)
Urospora penicilliformis (Roth) Areschoug	11, 17a	5–18, 20, 22, 23, 26 (64%)
Urospora wormskjoldii (Mertens in Hornemann) Rosenvinge	11	7, 8, 22 (11%)
TOTAL GREEN ALGAL TAXA	32	33
COMBINED TOTAL GREEN ALGAL TAXA (41)		
PHAEOPHYCEAE		
Agarum clathratum Dumort.	11, 15, 21, 22, X	7, 13–15, 22, 23 (21%)
Alaria esculenta (L.) Greville	11, 15, 21, 22	6–8, 10–12, 14, 22, 23 (32%)
Ascophyllum nodosum (L.) Le Jolis	11, 15, X	1, 2, 4–8, 10–28 (93%)
Ascophyllum nodosum (L.) Le Jolis ecad *scorpioides* (Reinke) Hauck		1, 2, 16, 19, 20, 24, 26, 28 (29%)
Asperococcus fistulosus (Hudson) Hooker	15	(0%)
Chorda filum (L.) Stackhouse	15, 17a	(0%)
Chorda tomentosa Lyngbye		14 (4%)
Chordaria flagelliformis (O. F. Müller) C. Agardh	11, 15, 21, 22	11, 12, 14 (11%)
Desmarestia aculeata (L.) J. V. Lamouroux	17a, 21, 22	15 (4%)
Desmarestia viridis (O. F. Müller) J. V. Lamouroux	15, 17a	8, 15, 16 (11%)
Dictyosiphon foeniculaceus (Hudson) Greville	15, 17, 17a, 21, 22	6, 7, 11, 12 (14%)
Dictyosiphon macounii Farlow	17a	(0%)
Ectocarpus fasciculatus Harvey	13a, 15, 17a, 21, 22	7, 11, 17, 22 (14%)
Ectocarpus siliculosus (Dillwyn) Lyngbye	15, 17a, 21	14 (4%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Elachista chondrii Areschoug		11 (4%)
Elachista fucicola (Velley) Areschoug	11, 14a, 15, 21, 22, X	5, 6, 10–13, 15, 17, 22, 28 (36%)
Eudesme virescens (Carm. ex Harvey in Hooker) J. Agardh	15, 17a	(0%)
Fucus distichus (L.) emend. Powell ssp. *anceps* (Harvey et Ward ex Carruthers) Powell		10, 14 (7%)
Fucus distichus (L.) emend. Powell ssp. *distichus* Powell	5a, 11, 15	5–7, 9–12, 14, 15, 22, 23 (39%)
Fucus distichus (L.) emend. Powell ssp. *edentatus* (Bach. Pyl.) Powell	11, 17a, 22	6–12, 15, 22, 23 (36%)
Fucus distichus (L.) emend. Powell ssp. *evanescens* (C. Agardh) Powell	11, X	11, 13, 15, 17 (14%)
Fucus spiralis L.	21	1, 5, 6, 10–15, 17, 18, 22–24 (50%)
Fucus vesiculosus L.	11, 21, X	1, 2, 4–13, 15–20, 22–28 (86%)
Fucus vesiculosus L. f. *limicola* Collins		1, 2, 28 (11%)
Gononema aecidioides (Rosenvinge) P. M. Pedersen	21	(0%)
Laminaria digitata (Hudson) J. V. Lamouroux	11, 15, 17a, 22, X	6, 7, 10–12, 14, 16, 22 (29%)
Laminaria longicruris Bach. Pyl.	21	17 (4%)
Laminaria saccharina (L.) J. V. Lamouroux	17a, X	10–13, 22, 23 (21%)
Leathesia difformis (L.) Areschoug	11, 15, 22	11 (4%)
Melanosiphon intestinalis (Saunders) Wynne		28 (4%)
Myrionema corunnae Sauvageau		14, 22 (7%)
Myrionema magnusii (Sauvageau) Loiseaux	15, 17a	(0%)
Myrionema strangulans Greville	14a, 15, 17a	(0%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Petalonia fascia (O. F. Müller) Kuntze	11, 15, 16	3–7, 10, 12–18, 21–23, 26 (61%)
Petroderma maculiforme (Wollny) Kuckuck		3, 16, 25 (11%)
Pilayella littoralis (L.) Kjellman	11, 15, X	3–5, 8, 11–18, 20, 26, 28 (54%)
Pseudolithoderma extensum (P. et H. Crouan) S. Lund		13, 20 (7%)
Punctaria latifolia Greville	15, 17a, 21	(0%)
Punctaria tenuissima (C. Agardh) Greville	15, 17a, 21	(0%)
"*Ralfsia bornetii* Kuckuck"	15	3, 4, 7, 15, 16, 18, 23 (25%)
"*Ralfsia clavata* (Carmichael) Crouan *sensu* Farlow"	15	2, 11, 15, 21, 28 (18%)
Ralfsia fungiformis (Gunnerus) Setchell et N. L. Gardner	21, 22	(0%)
Ralfsia pusilla (Strömfelt) Batters	21, 22	(0%)
Ralfsia verrucosa (Areschoug) J. Agardh	11, X	1, 4, 5, 10, 11, 15, 16, 20–23, 25, 27, 28 (50%)
Saccorhiza dermatodea (Bach. Pyl.) J. Agardh	11, 14a, 15, 22	10, 11, 14 (11%)
Scytosiphon simplicissimus (Clemente) Cremades	11, 15, 21, X	3–7, 10–18, 21–23, 26–28 (71%)
Sphacelaria cirrosa (Roth) C. Agardh	17a	6, 11 (7%)
Sphacelaria radicans (Dillwyn) C. Agardh	15	(0%)
Spongonema tomentosum (Hudson) Kützing		11 (4%)
Stictyosiphon griffithsianus (Le Jolis) Holmes et Batters	17a	(0%)
TOTAL BROWN ALGAL TAXA	40	37
COMBINED TOTAL BROWN ALGAL TAXA (50)		
RHODOPHYCEAE		
Ahnfeltia plicata (Hudson) Fries	15, 22	7, 11, 12, 22 (14%)
Antithamnionella floccosa (O. F. Müller) Whittick	11	14, 17 (7%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Audouinella alariae (H. Jónsson) Woelkerling	15, 22	(0%)
Audouinella daviesii (Dillwyn) Woelkerling	16, 17a	(0%)
Audouinella membranacea (Magnus) Papenfuss	15	13, 23 (7%)
Audouinella purpurea (Lightfoot) Woelkerling	15, 17a, 21a	6, 11, 14 (11%)
Audouinella secundata (Lyngbye) P. Dixon in M. Parke et P. Dixon		5, 11, 12, 22 (14%)
Bangia atropurpurea (Roth) C. Agardh	11, 15	6–8, 10, 12, 14, 15, 17, 22 (32%)
Callithamnion tetragonum (Withering) S. F. Gray		2 (4%)
Callophyllis cristata (C. Agardh) Kützing	15	10, 15, 22 (11%)
Ceramium deslongchampii Chauvin ex Duby	15, 22	6, 10 (7%)
Ceramium nodulosum (Lightfoot) Ducluzeau	11, 15, 21, 22	6–8, 10–12, 14, 15, 22 (32%)
Chondrus crispus Stackhouse	5a, 11, 15, X	2, 4–18, 22–24, 26–28 (79%)
Choreocolax polysiphoniae Reinsch	15	12 (4%)
Clathromorphum circumscriptum (Strömfelt) Foslie	11, 15, 22, X	4, 5, 7, 11, 13, 15, 16, 22, 23 (32%)
"*Conchocelis rosea* Batters"	15	(0%)
Corallina officinalis L.	5a, 11, 15, 17, 21, 21b, 22	5–7, 9–14, 16, 22, 23 (43%)
Cystoclonium purpureum (Hudson) Batters	15, 17a	15, 23 (7%)
Devaleraea ramentacea (L.) Guiry	11, 15, 22	6–8, 10–12, 14, 15, 22, 23 (36%)
Dumontia contorta (S. G. Gmelin) Ruprecht	22	1, 4, 7–9, 13, 15–18, 22, 23, 28 (46%)
Erythrotrichia carnea (Dillwyn) J. Agardh		13 (4%)
Fimbrifolium dichotomum (Lepechin) G. I. Hansen	15, 17a, 22	(0%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Gloiosiphonia capillaris (Hudson) Carmichael ex Berkeley	15, 16, 22	(0%)
Gymnogongrus crenulatus (Turner) J. Agardh	21, 22	(0%)
Hildenbrandia rubra (Sommerfelt) Meneghini	21, X	1, 2, 7, 11, 13, 15, 17, 20, 22, 25, 27, 28 (43%)
Lithothamnion glaciale Kjellman	17a, 22, X	22, 23 (7%)
Mastocarpus stellatus (Stackhouse in Withering) Guiry in Guiry et al.	11, 15, 17a, 22, X	5–15, 17, 21–23 (54%)
Membranoptera alata (Hudson) Stackhouse	15	22 (4%)
Nemalion helminthoides (Velley in Withering) Batters	15, 22	(0%)
Palmaria palmata (L.) Kuntze	11, 15, 17a, 22, X	6, 7, 10–12, 14, 22, 23 (29%)
"*Petrocelis cruenta* J. Agardh"	11, 14a, 15, 21a, 22, X	6, 8, 11, 13, 14, 22, 23 (25%)
Peyssonnelia rosenvingii F. Schmitz in Rosenvinge	15	(0%)
Phycodrys rubens (L.) Batters	15, 22	22 (4%)
Phyllophora pseudoceranoides (Gmelin) Newroth et A. Taylor		22 (4%)
Phymatolithon lenormandii (Areschoug in J. Agardh) Adey	15, 21, X	2, 7, 15 (11%)
Phymatolithon tenue (Rosenvinge) Düwel et Wegeberg	15	22, 23 (7%)
Plumaria plumosa (Hudson) Kuntze	15, 21	6, 12, 14 (11%)
Pneophyllum fragile Kützing	17a	(0%)
Polyides rotundus (Hudson) Greville	15, 22	(0%)
Polysiphonia flexicaulis (Harvey) Collins	11, 19, 21	1, 13 (7%)
Polysiphonia fucoides (Hudson) Greville	16	8, 15 (7%)
Polysiphonia harveyi J. Bailey	21	2, 11 (7%)
Polysiphonia lanosa (L.) Tandy	11, 15, 21, X	5–8, 10–15, 17, 18, 22, 23 (50%)
Polysiphonia stricta (Dillwyn) Greville	15, 17a	6, 8–12, 14–16, 22, 23 (39%)

Table 1. Continued.

	Historical Collections	Present Collections (% Occurrence)
Porphyra amplissima (Kjellman) Setchell et Hus	15	4 (4%)
Porphyra leucosticta Thuret in Le Jolis	11	6, 8, 10, 12, 22 (18%)
Porphyra linearis Greville		9, 10, 22 (11%)
Porphyra miniata (C. Agardh) C. Agardh	15	(0%)
Porphyra purpurea (Roth) C. Agardh		12 (4%)
Porphyra umbilicalis (L.) J. Agardh	11, 15, 22	5, 6, 8, 10–12, 14, 15, 22 (32%)
Ptilota serrata Kützing	15, 21, 22	16 (4%)
Rhodomela confervoides (Hudson) P. C. Silva	21, 22	5, 10–12, 14, 15, 22 (25%)
Scagelia pylaisaei (Montagne) M. J. Wynne	15	(0%)
Titanoderma corallinae (P. et H. Crouan) Woelkerling, Chamberlain et Silva	29	12 (4%)
Titanoderma pustulatum (J. V. Lamouroux) Woelkerling, Y. M. Chamberlain et P. C. Silva	15	11, 13 (7%)
TOTAL RED ALGAL TAXA	49	43
COMBINED TOTAL RED ALGAL TAXA (55)		
TOTAL SEAWEED TAXA	121	113
COMBINED SEAWEED TAXA (146)		

sibility of shorelines by foot; (2) habitat representation and diversity; (3) coverage of the entire island; and (4) previous historical collections. With the exception of a few localized summer collections made during the mid-1960s, the recent collections were made between 1993 and 1996 (Appendix). We made comprehensive seasonal collections of all conspicuous seaweeds at most sites in order to enumerate spatial and temporal patterns (Druehl 1981). Seaweeds were either pressed immediately or transferred within 24–36 hours to the University of New Hampshire where they were processed and identified. Several references were utilized for identification (Adey and Adey 1973; Bird and McLachlan 1992; Blair 1983; Bliding 1963, 1968; Burrows 1991; Dixon and Irvine 1977; Düwel and Wegeberg 1996; Farlow 1881; Fletcher 1987; Hoek 1963, 1982; Irvine 1983; Irvine and Chamberlain 1994; Kingsbury 1969; Maggs and Hommersand 1993; Schneider and Searles 1991; Sears 1998; Taylor 1957; Villalard-Bohnsack 1995; Webber and Wilce 1971; Woelkerling 1973; Wynne and Heine 1992). The nomenclature primarily follows South and Tittley (1986), except for several recent papers noted above. Collections were documented by depositing approximately 1200 voucher specimens in the Albion R. Hodgdon Herbarium at the University of New Hampshire (NHA).

Collections from the last century were also evaluated (>300 specimens), including those of Frank Shipley Collins and Isaac Holden (cf. Appendix). Many of these are deposited in the Farlow Herbarium (FH) of Harvard University, the Daniel C. Eaton Herbarium of the Peabody Museum at Yale University (YU), and the New York Botanical Garden (NY) and Brooklyn Botanic Garden (BKL). Specimens contained within *Phycotheca Boreali-Americana* are also particularly important in making historical comparisons of Mount Desert's marine algal flora (Setchell 1925; Taylor 1957).

Two floristic assessments of Mount Desert seaweeds are made. First, the number and percentage of taxa in common to each of the 28 present study sites (Figures 4–7) are given, with the latter values (C) determined by using Czekanowski's coefficient (Bray and Curtis 1957; Mathieson et al. 1996). Second, a comparison of historical and present records of taxa at three sites (Otter Cliffs, Seal Harbor, and the Seawall-Southwest Harbor area) is given, as well as for Mount Desert Island as a whole (Figure 2, 8).

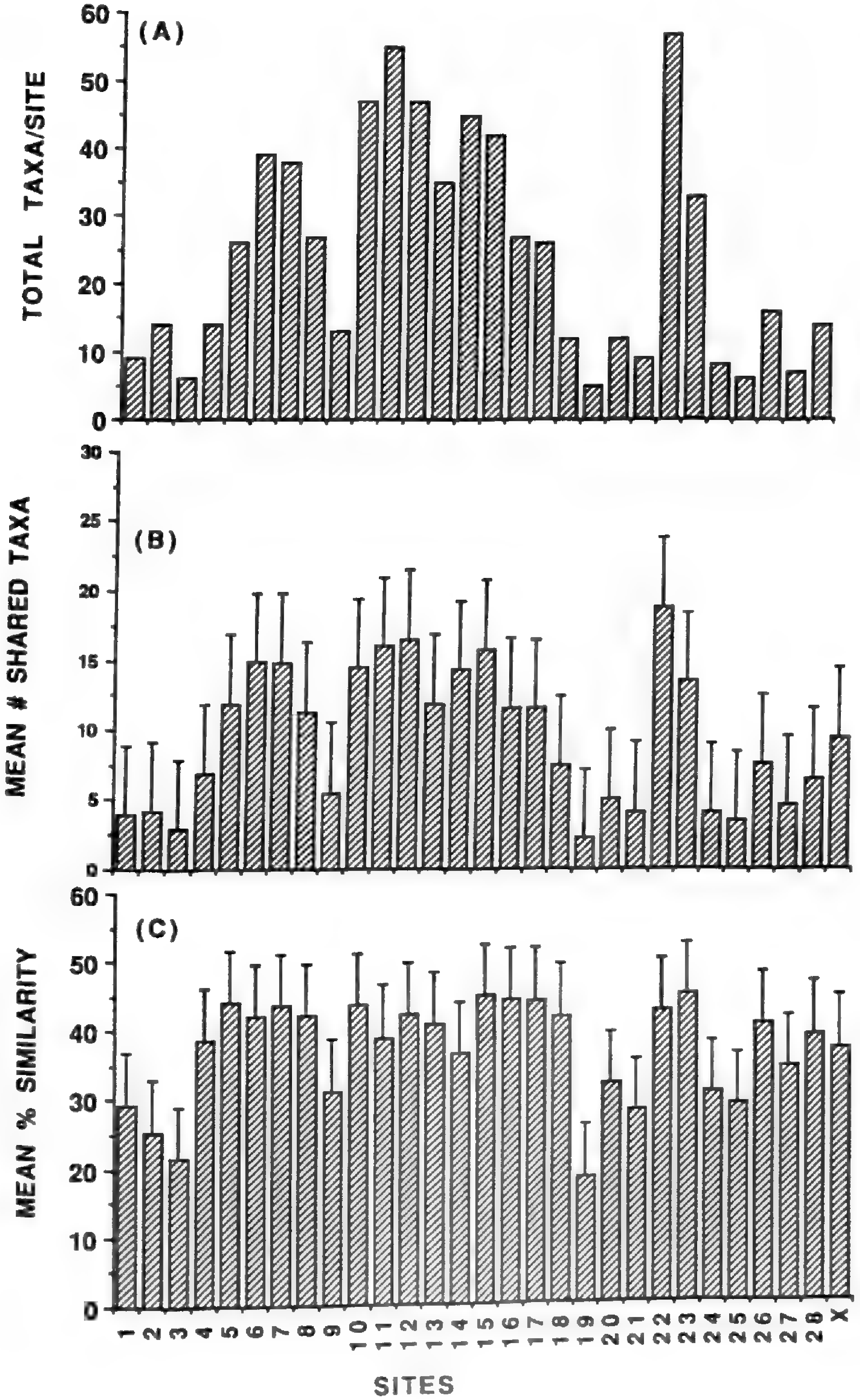

Figure 4. A comparison of the seaweed floras from 28 study sites on Mount Desert Island, expressed as total number of taxa (A), the mean (±S. D.) number of shared taxa (B), and mean % (±S. D.) similarity per site (C). x = mean of all sites.

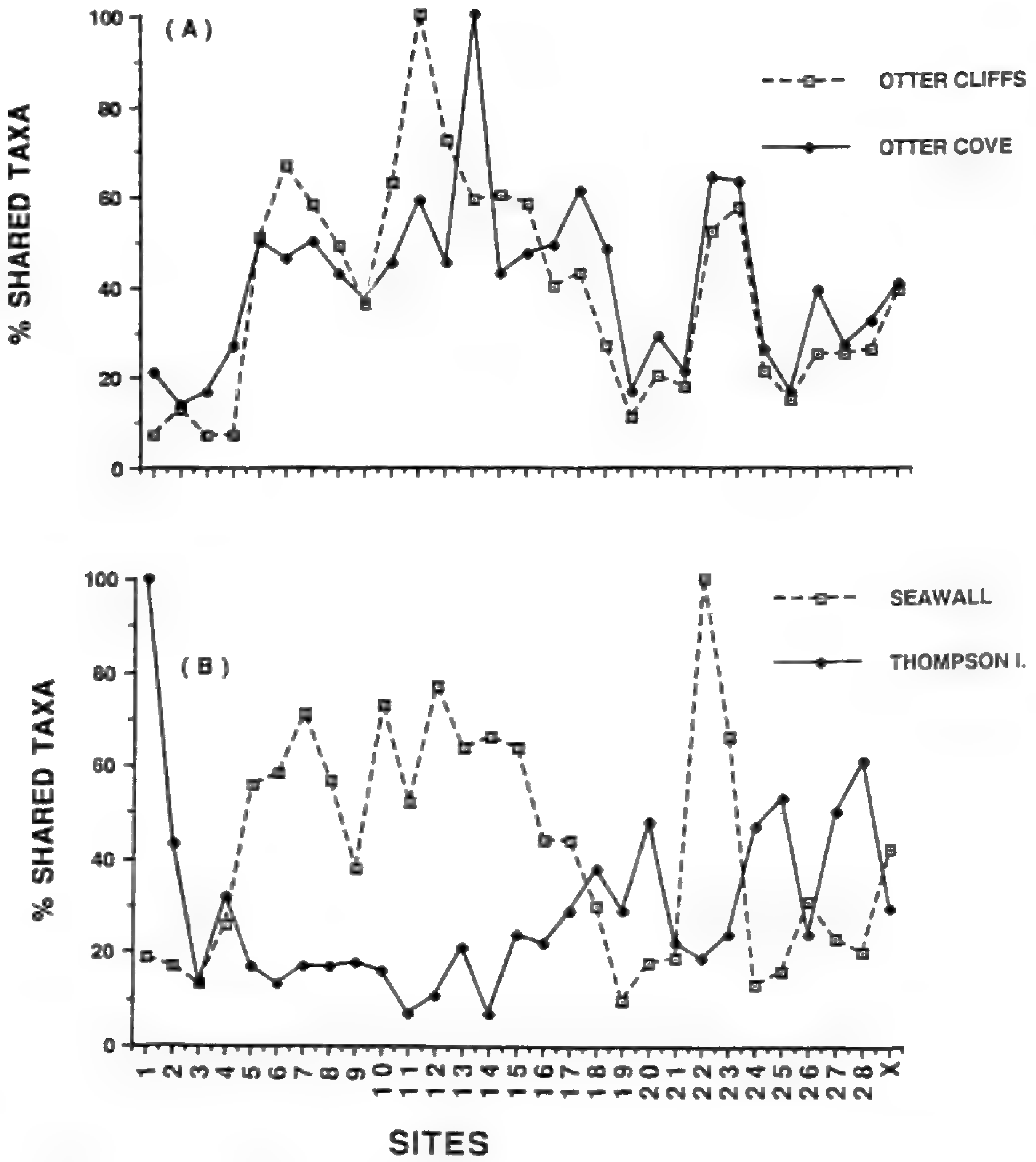

Figure 5. Floristic similarities of four study sites on Mount Desert Island, Otter Cliffs and Otter Cove (A) and Seawall and Thompson Island (B), expressed as the percentage of shared taxa with each of the other 27 study sites. x = mean of all sites.

Zonation studies. The vertical distribution of seaweeds and selected invertebrates at Otter Cliffs, Otter Cove, and Thompson Island (Figure 2, 3; Table 2) was documented during the summer and fall of 1996, 74 years after the initiation of Johnson and Skutch's (1928a, b, c) classical studies at Otter Cliffs (Figure 3A). Before beginning our zonation studies, their original benchmark, which was established in 1923, was re-located; it is embedded within an exposed outer rock at +5.7 m above MLW (Figure 3A,

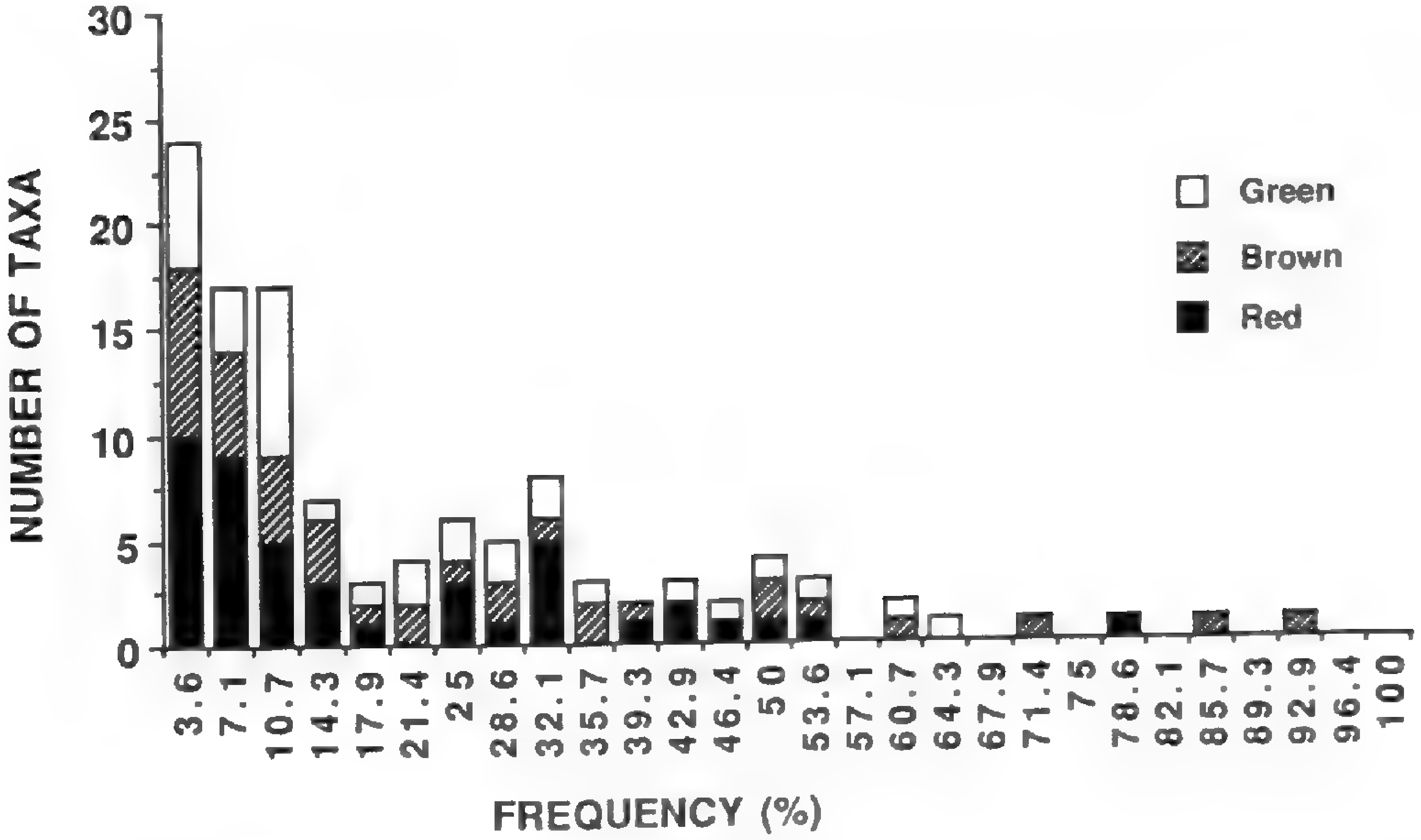

Figure 6. Frequency distribution pattern of 113 Mount Desert Island taxa recorded from 28 present study sites. Taxa found at only one site (3.6% occurrence) are represented by the left-most bar of the graph; those at two sites by the next bar (7.1%), etc.

arrow). Present elevation measurements were related to their datum point, with its height being confirmed after making multiple measurements (plumbing) from the surface to the predicted low tide of that day. A line level and stadia rod were used to make height measurements by pulling a "leveled" line from the benchmark or from secondary reference points. Accuracy of the present elevational measurements is estimated to be ± 5.0 cm. Upper and lower limits of all conspicuous algae are recorded, as well as those for selected invertebrates (e.g., *Semibalanus balanoides*). Some seaweeds were collected for critical identifications in the laboratory. Similar field procedures were used to characterize the biological zones at two other Mount Desert sites (Otter Cove and Thompson Island; Figure 3B, C), while published records from an exposed site in southern Maine (Bald Head Cliff, York) and a semi-exposed site in New Hampshire (Jaffrey Point, Newcastle) were also compared (Femino and Mathieson 1980; Mathieson et al. 1981).

Otter Cliffs (44° 18.58′ N, 68° 11.44′ W), the most exposed of the three Mount Desert zonation sites, is located on the eastern side of Otter Point, approximately 50 km from the Bay of Fundy.

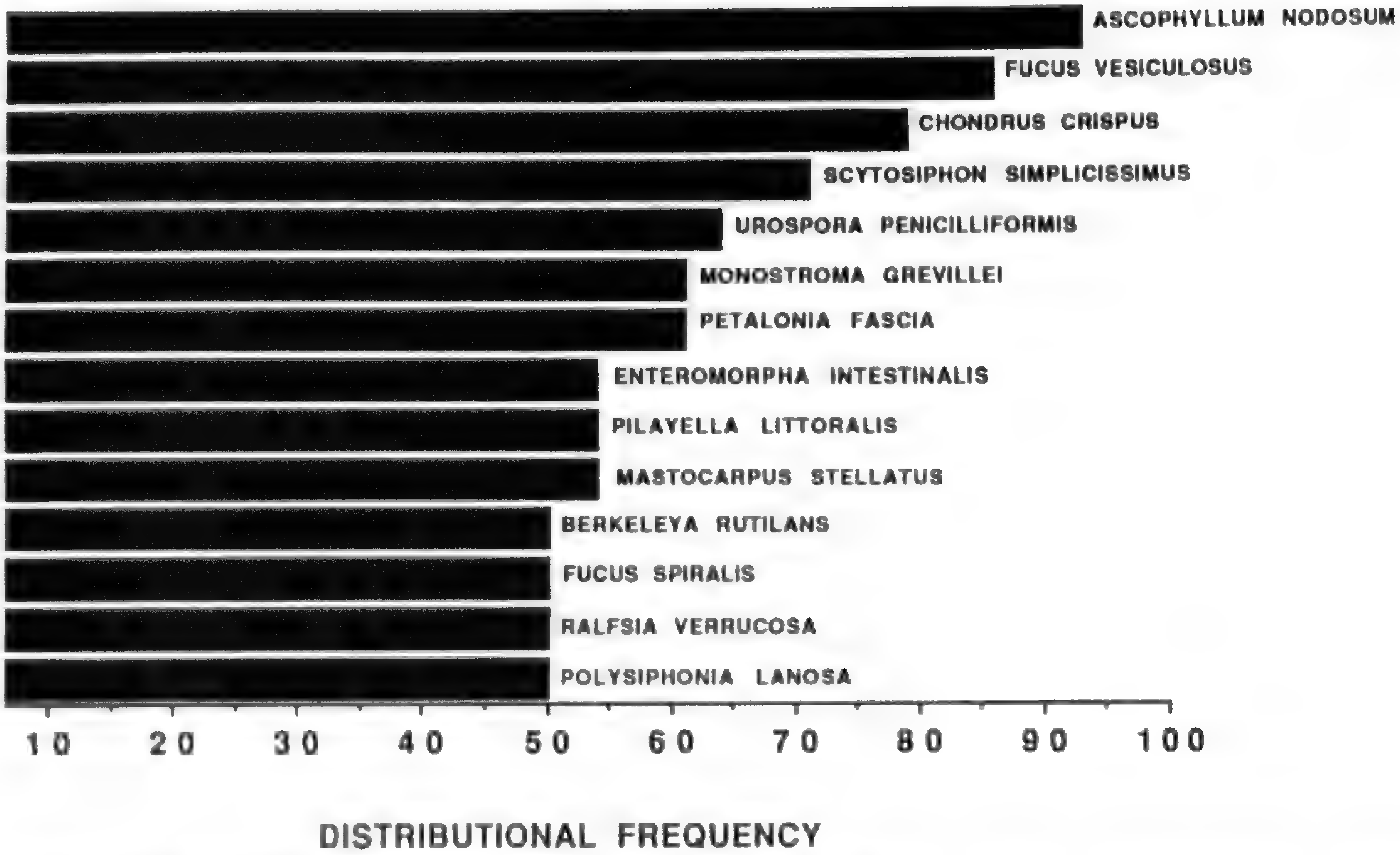

Figure 7. Distributional frequency (%) of the thirteen most common seaweed taxa, plus the benthic colonial diatom *Berkeleya rutilans*, at the 28 present study sites.

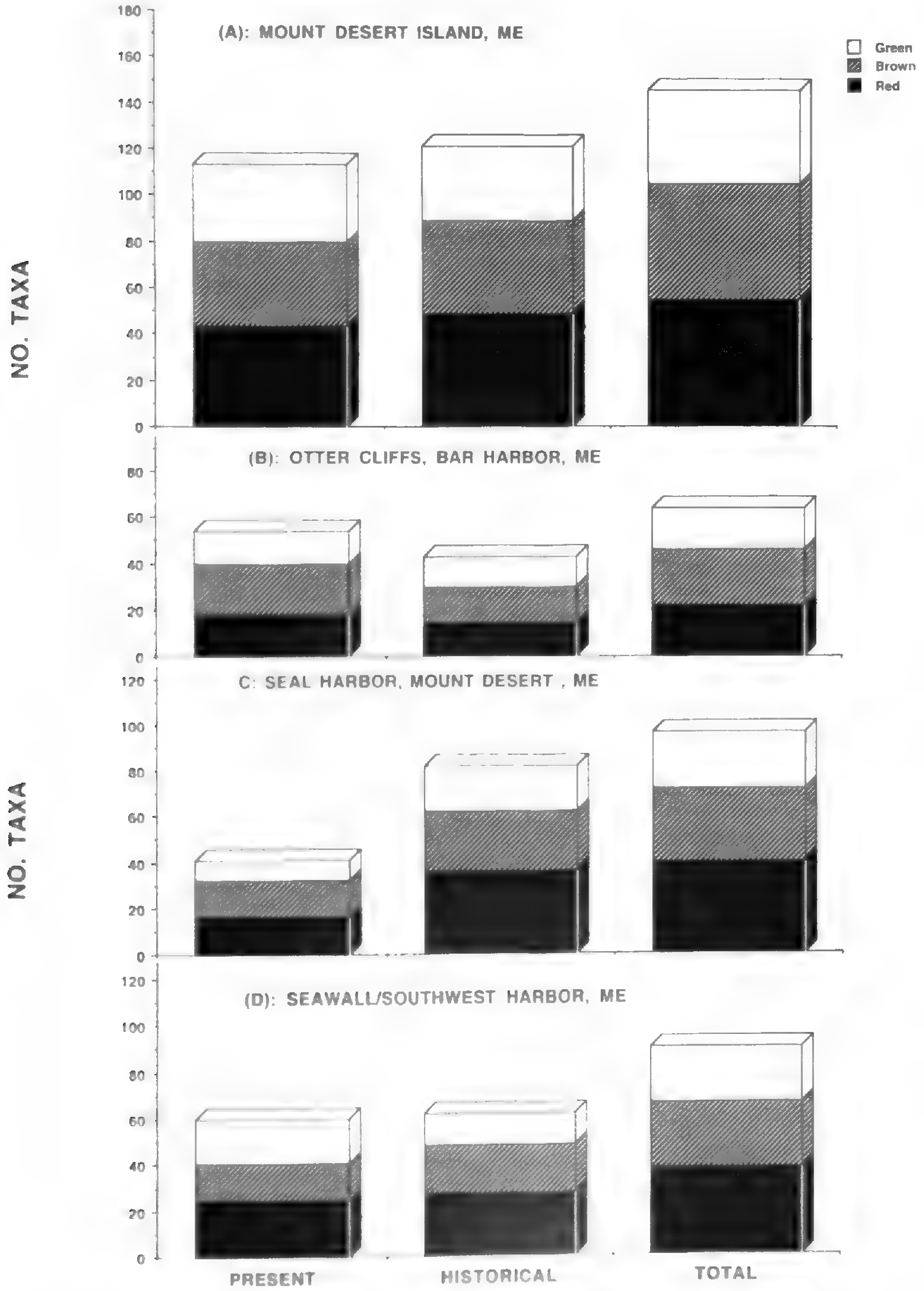

Figure 8. A comparison of present, historical, and combined total seaweed taxa (green, brown, and red) from 28 Mount Desert Island sites (A) and an analogous comparison for three sites: Otter Cliffs (B), Seal Harbor (C), and the Seawall-Southwest Harbor area (D).

Table 2. Zonation comparisons (m above or below MLW) at seven sites in Maine and New Hampshire. Key to symbols: (1) Otter Cliffs, ME—exposed & semi-exposed (Johnson & Skutch, 1928a, b, c); (2) Otter Cliffs, ME—exposed outcrop (1996); (3) Otter Cliffs, ME—semi-exposed site (1996); (4) Otter Cove, ME—sheltered (1996); (5) Thompson I., ME—sheltered (1996); (6) Bald Head Cliff, ME—exposed (1980); (7) Jaffrey Point, NH—semi-exposed (1981); () = tide pool; (−) = subtidal; * = five intertidal species of *Verrucaria* are recorded from this area, with the dominant taxon being *V. striatula* Wahlenberg.

	1	2	3	4	5	6	7
CHLOROPHYCEAE							
Acrochaete viridis (Reinke) (R. Nielsen)							0.0–0.6
Blidingia minima	(1.9) 3.7–5.0		1.8–4.0	3.0–3.2			
Capsosiphon fulvescens							2.2–2.7
Chaetomorpha brachygona							0.0–0.6
Chaetomorpha linum							0.0–0.6
Chaetomorpha melagonium			(1.2)				(−0.2)
Chaetomorpha picquotiana							0.0–0.6
Chlorochytrium cohnii Wright							2.0
Cladophora sericea	(1.2)		(1.2)–1.8 (2.1)				2.2–2.7
"*Codiolum petrocelidis*"							0.3
"*Codiolum pusillum*"	1.7–4.5		2.4–4.0	2.6–3.0			2.0–3.4
Enteromorpha clathrata							2.2–2.7
Enteromorpha compressa	0.9–4.3						
Enteromorpha flexuosa ssp. *paradoxa*							2.2–2.7
Enteromorpha intestinalis	(1.2)		(1.2) 1.5–2.9	3.2		1.8–2.8 (4.7)	2.2–2.7
Enteromorpha linza							0.0–0.5
Enteromorpha prolifera							2.2–2.7

Table 2. Continued.

	1	2	3	4	5	6	7
Enteromorpha torta							2.2–2.7
Epicladia flustrae							0.0–2.2
Monostroma grevillei	2.1–4.3					1.3–2.3	0.0–1.7
Mougeotia sp.	4.3–9.2						
Percursaria percursa							2.2–2.7
Prasiola stipitata		5.4–5.7					2.7–3.3
Protomonostroma undulatum f. *pulchrum*						1.0–1.8	0.0–0.9
Rhizoclonium riparium							2.2–2.7
Rhizoclonium tortuosum	0.6–2.1		(1.2)–(3.4)	(1.0)–(1.8)		1.8–2.2	0.0–0.6
Spongomorpha arcta	0.6–2.5 (3.4)		0.1–0.5 (2.1)			0.0–1.9	0.0–0.2
Spongomorpha spinescens	0.0–2.1 (2.7)		0.1–0.5			0.0–(1.8)	0.0
Ulothrix flacca	(1.2) 3.1–4.3						0.8–2.8
Ulothrix speciosa						1.8–3.0	2.5–2.8
Ulva lactuca	0.0–0.9	(3.0)	0.0–1.8 (3.4)	0.0–(1.0)		0.0–1.8	0.0
Ulvaria obscura		0.0–1.0 (3.0)	0.0–0.4 (3.4)			1.3–1.6 (1.8)	0.0–0.5
Urospora penicilliformis	0.6–5.0		2.4–4.0	2.4–3.1		1.8–3.0	1.3–2.5
Urospora wormskjoldii						1.8–3.0	
PHAEOPHYCEAE							
Agarum clathratum	(1.2)			−0.6–(0.4)			0.0–0.2
Alaria esculenta	0.0–0.6 (0.8)	0.0–0.7	0.0 (2.1)			0.0–0.9 (1.8)	0.0
Ascophyllum nodosum	0.6–2.7 (3.5)	(3.5)	0.6–2.8 (3.4)	0.2–2.0	0.2–2.9	1.4–2.3	0.0–2.0
Ascophyllum nodosum ecad *scorpioides*					2.0–2.5		
Chordaria flagelliformis	0.5–2.1		(2.0)–(3.4)				0.0–0.1
Dictyosiphon foeniculaceus			(2.0)				0.0

Table 2. Continued.

	1	2	3	4	5	6	7
Ectocarpus siliculosus							0.0
Elachista chondrii			0.1				
Elachista fucicola	0.6–2.5	0.3	0.1–1.5 (3.4)	0.5–2.0			0.0–2.0
Fucus distichus ssp. *distichus*	2.1–4.3	(3.4)–(3.5)	(3.4)			1.2–1.8	0.9–2.2
Fucus distichus ssp. *edentatus*	0.6–2.5	0.3–2.0	0.1 (1.2)				0.0–0.5
Fucus distichus ssp. *evanescens*			0.0–0.6 (2.1)	0.0–(0.4)			0.0–0.5
Fucus spiralis			2.8–4.3	1.9–2.8	2.4–3.5		2.3–2.7
Fucus vesiculosus	1.5–4.5		0.1–3.0	0.0–2.0	0.0–0.8	0.0–1.8	0.0–2.3
Fucus vesiculosus f. *limicola*					2.0–2.5		
Laminaria digitata	0.0–0.5		0.0–(1.2)				0.0–0.1
Laminaria saccharina	(0.8)		0.0–(2.1)	0.0–(0.4)			0.0–0.1
Laminariocolax tomentosoides (Farlow) Kylin							0.0
Leathesia difformis	(1.9)		(1.2)			1.7–2.0	0.0–0.5
Myrionema corunnae							0.0
Petalonia fascia	0.0–1.5 (3.2)			(1.0)–(1.2)		1.5–2.0	0.3–2.2
Petalonia zosterifolia (Reinke) Kuntze							0.0
Pilayella littoralis	0.0–1.5		(1.7)–(2.1)	0.5–1.0 (1.6)			0.0–1.3
Pseudolithoderma extensum				0.0–(1.8)			0.0
"*Ralfsia clavata*"		(3.5)					0.0–0.4
Ralfsia verrucosa	0.6–4.3		(1.2)–(3.5)		−0.2	1.7–2.2 (4.8)	0.0–2.2
Saccorhiza dermatodea	0.0–0.3 (0.8)						0.0–0.1
Scytosiphon simplicissimus			(1.7)–(2.0)	(0.4)–(1.8)			0.3–2.7
Sphacelaria cirrosa			0.4–(2.0)				0.2–1.4

Table 2. Continued.

	1	2	3	4	5	6	7
Ulonema rhizophorum Foslie							0.0–2.5
RHODOPHYCEAE							
Ahnfeltia plicata		0.0–(3.0)	(1.2)				0.0–0.6
Antithamnionella floccosa	(0.6)					(−0.2)–(1.8)	0.0
Audouinella membranacea							0.0–2.0
Audouinella purpurea			(2.0)				0.0–1.3
Audouinella secundata							0.0–1.9
Bangia atropurpurea	1.4–4.1					1.8–3.0	0.6–2.8
Bonnemaisonia hamifera Hariot							0.0
Callocolax neglectus F. Schmitz ex Batters							0.0
Callophyllis cristata							0.0
Ceramium deslongchampii							0.0–0.3
Ceramium nodulosum	(3.4)		0.0–(3.4)			0.0–1.8	0.0–0.5
Ceratocolax hartzii Rosenvinge							0.0
Chondrus crispus	0.0–0.8 (2.7)	0.0–(3.0)	0.0–0.9 (3.4)	0.0–(1.8)		0.0–2.2 (4.8)	0.0–2.1
Choreocolax polysiphoniae Reinsch							0.2–2.0
Clathromorphum circumscriptum	0.0–0.6 (3.4)	0.0–1.0 (3.0)	0.0–(2.6)	0.0–(1.8)		0.0–(1.8)	0.0–2.8
Coccotylus truncatus (Pallas) M. J. Wynne et J. M. Heine							0.0
Corallina officinalis	(3.4)		0.0–(3.4)	0.0–(1.8)			0.0–0.1
Cystoclonium purpureum							0.0–0.2
Devaleraea ramentacea	0.0–0.8 (3.4)	0.0–1.0 (3.0)	0.0–0.4 (3.4)			0.0–1.0 (1.8)	0.0–0.1
Dumontia contorta				(0.4)–(1.8)	0.0–0.2		0.0–2.5

Table 2. Continued.

	1	2	3	4	5	6	7
Erythrodermis traillii (Holmes ex Batters) Guiry et Garbary							0.0
Erythrotrichia carnea				0.0–(2.1)			0.0–0.6
Gymnogongrus crenulatus							0.0
Hildenbrandia rubra		(3.5)	0.0–(3.5)	0.0–0.5 (1.6)	0.0–0.2	0.0–2.2 (4.8)	0.0–0.6
Lithothamnion glaciale							0.0–0.4
Mastocarpus stellatus	2.5	0.0–0.7	0.0–2.0	0.1–(1.2)		0.0–2.2	0.0–2.5
Palmaria palmata	0.0–2.5	0.0–0.8 (1.0)	0.0–1.5 (2.1)			1.6–1.8	0.0–0.1
"*Petrocelis cruenta*"		0.0–1.0	0.0–0.4 (2.1)	0.0–(1.8)		0.0–1.8	0.0–0.3
Peyssonnelia rosenvingii							0.0–0.3
Phycodrys rubens							0.0–0.2
Phyllophora pseudoceranoides							0.0
Phymatolithon foecundum (Kjellman) Düwel et Wegeberg							0.0
Phymatolithon lenormandii							0.0–0.3
Phymatolithon tenue							0.0
Plumaria plumosa							0.0–1.3
Pneophyllum fragile Kützing							0.0
Polysiphonia elongata							0.0
Polysiphonia flexicaulis				0.0–(2.1)	0.0–0.2		0.0
Polysiphonia lanosa	1.8–3.0		0.6–2.5	0.0–1.2			0.0–2.0
Polysiphonia nigra (Hudson) Batters							0.0
Polysiphonia stricta	0.0–2.5	0.0–1.0					0.0–0.4
Porphyra leucosticta	2.1						0.0–2.4
Porphyra miniata							0.0–0.2
Porphyra umbilicalis	0.6–3.5	0.8–1.4	0.0–3.0				0.0–2.5

Table 2. Continued.

	1	2	3	4	5	6	7
Porphyridium purpureum (Bory) Drew et Ross	4.3–9.2						
Rhodomela confervoides			0.0–(1.2)				0.0–0.3
Titanoderma corallinae							0.0–0.1
Titanoderma pustulatum							0.0–0.5
BACILLARIOPHYCEAE							
Berkeleya rutilans			(1.2)	(0.4)–(1.2)			
CYANOPHYCEAE							
Calothrix fasciculata	4.3–9.2						
Calothrix scopulorum	2.1–4.9						
Oscillatoria sp.	4.3–9.2						
LICHENS							
Verrucaria spp.*	2.1–4.3		3.5–6.3	0.5–6.5	0.0–4.0		
SPERMATOPHYTA							
Zostera marina				(1.4)			
ANIMALS							
Mytilus edulis		0.3–1.0 (3.5)	0.8–(3.5)	0.0–(1.8)		0.0–3.0	
Semibalanus balanoides		0.3–3.8 (4.4)	0.0–3.5	1.3–2.8	0.7–3.2	1.5–3.4	0.1–2.7
Serpulid				(1.4)			
Strongylocentrotus droebachiensis			(1.2)–(2.0)	0.0–(1.4)			

Its granitic outcrops, which are the highest ocean cliffs on the U. S. Atlantic coast (Butcher 1987), jut directly south into the North Atlantic, exposing it to extreme northeastern storms and waves that reach or exceed 6 m (Figure 3A). Two distinct habitats are evident: a highly exposed cluster of outer rocks that is accessible only at extremely low tides and a nearby semi-exposed vertical cliff. Johnson and Skutch (1928a, b, c) presented composite data for the site. Otter Cliffs and Otter Cove (Figure 3B) have an identical tidal amplitude (4.6 m). Otter Cove (44° 18.79′ N, 68° 11.89′ W) is a moderately protected open coastal habitat about 0.5 km west of Otter Cliffs, on the opposite side of Otter Point (Figure 2). Its granitic outcrops have a more horizontal contour than those at Otter Cliffs. Thompson Island (44° 25.58′ N, 68° 22.07′ W), located 20 km northwest of Otter Cliffs, is a protected two-hectare island within Mount Desert Narrows (Figure 2). It has a greater tidal amplitude than the other two sites (approximately 5 m); its substratum consists of pebbles, sand, and mud scattered amongst a few granitic outcrops. There is also a restricted fringing marsh (Figure 3c).

HABITAT DESCRIPTION AND HISTORY

Mount Desert Island, which is located northeast of Penobscot Bay (Figure 1), is the third largest insular environment on the East Coast of the United States and the largest in Maine (Platt 1996; Simpson 1987). It covers approximately 173 km^2 (ca. 26,058 ha), has a perimeter of about 64,390 km, and maximum length and width of 24 and 19 km, respectively. The Cranberry Isles, plus Swans and Long Islands, all lie to the south and southwest of Mount Desert (Figure 1, 2). Biologically, Mount Desert is situated near the boundary of the Boreal (Canadian) and Austral regions and contains a mixture of northern and southern species (Anonymous 1991, 1992; Butcher 1987; Moore 1921; Proctor 1927, 1938, 1946; Rand and Redfield 1894; Simpson 1987).

The island's coastline is composed primarily of granitic rock, with many shorelines consisting of sloping ledges of crystalline granite made up of quartz, feldspar, and other minerals (Butcher 1987). The island's diverse and irregular coastline ranges from exposed and semi-exposed open coastal sites, to hectares of protected waters, extensive mudflats, and salt marshes. The south shore between Schooner Head and East Point (including Otter

Cliffs), plus the area from Seawall to Bass Harbor Head, is most exposed to the open Atlantic (Figure 2; Appendix). Protected open coastal habitats are interspersed among the exposed ones, particularly within the embayed waters behind the Cranberry Isles, Somes Sound, Seal Harbor, Northeast Harbor, Southwest Harbor, and Manset Harbor (Proctor 1927; Rand and Redfield 1894).

Somes Sound (Figure 2) is a unique site topographically and historically. It is a long, sheltered arm located within the center of the island (approximately 8 km), dividing the island into two major peninsulas. Geologically, it represents a narrow, glacially carved trough that extends north to south, roughly parallel to the Pleistocene ice advance in this area (Butcher 1987; Johnson 1925). Because of its pronounced topographic coastal relief, which may reach 250 m above sea level, it has been referred to as the only fjord on the east coast of the United States (Chapman 1970; Condon 1994; Johnson 1925, 1987); however, its low freshwater input and lack of stratification are typical of other shallow Maine estuaries (McAlice 1977; Pettigrew et al. 1997). Summer surface water temperatures and salinities in Somes Sound, which are typical for the island as a whole, vary from 13.0–14.5°C and 31.7–31.9 ppt between the mouth and head, while spring temperatures are lower and salinities are not appreciably reduced (Ketchum and Cass 1986).

A shallow strait in the northwest part of the island, Mount Desert Narrows, connects the nearby Eastern and Western Bays that in turn merge with Blue Hill and Frenchman Bays (Figure 2). Two bridges connect Thompson Island to the mainland on the north and Mount Desert to the south. The open waters of Frenchman Bay on the eastern side of the island contain many small islands, which, along with Mount Desert, enclose a large body of water between them and the mainland to the north (Proctor 1927). Several rivers flow into Frenchman Bay, including the Jordan and Skillings. Some drain the adjacent terrain, while others are tortuous channels with swift currents due to tides with vertical ranges of 4.0 to 5.0 m. Frenchman Bay is different from the exposed waters to the south and Blue Hill Bay to the west. The latter is a sheltered and often muddy location fed by several large brooks and the Union River.

Mount Desert Island has long been a destination for explorers, travelers, and tourists (Morrison 1960, 1972; Simpson 1987).

Shell heaps testify to the presence of native American encampments dating back 6,000 years (Anonymous 1991, 1992; Butcher 1987; Condon 1994). The French explorer Samuel de Champlain provided the first positive description of Mount Desert in 1604 and correctly identified it as an island (Duncan et al. 1995; Simpson 1987). Champlain was so impressed with the bleak and barren grandeur of the glacially scoured mountains (Belknap et al. 1986; Butcher 1987; Kjerfve 1989) that he called it "Isles des Monts Desert" (Johnson 1987). The rise of Mount Desert as a resort destination occurred in the late 1800s, after such artists as Thomas Cole and Frederick Church began summering in Bar Harbor (Anonymous 1987, 1991, 1992; Butcher 1987; Simpson 1987; Tree and Roundy 1995). Naturalists, including John James Audubon and Louis Agassiz, found the island attractive because of its wide diversity of organisms, as well as its nearness to the boundary line between two ornithological and botanical zones (Simpson 1987).

The legislative history of Acadia National Park, which now comprises 12,950 hectares of Mount Desert Island (ca. 50%), officially began with the establishment of Sieur de Monts National Monument in 1916 (Anonymous 1991, 1992). The name was changed to Lafayette National Park in 1919 and ultimately to Acadia in 1929. An additional 13 km^2 (ca. 2,023 ha) of Acadia includes Isle au Haut (High Island) to the south and some parts of the Schoodic Peninsula to the north (Figure 1). Acadia is the only national park in the northeastern United States and is visited by several million people each year (>4.5 million in 1990). Overall, its popularity is second only to Yellowstone National Park and there is concern that anthropogenic impacts such as traffic and deteriorating air quality may cause irreparable damage within the park (Anonymous 1992, 1995; Eckert et al. 1994, 1997). Greene et al. (1992) emphasize the significance of historical resource inventories in evaluating possible environmental damage. The studies of benthic marine plants reported here are intended to supplement such historical inventories and contribute to the long-term monitoring of Acadia National Park and Mount Desert Island.

RESULTS

Present-day floristic patterns. A total of 113 seaweeds is recorded from the 28 present study sites, including 33 Chlorophyceae, 37 Phaeophyceae, and 43 Rhodophyceae (Table 1). In addition, the benthic colonial diatom *Berkeleya rutilans* (Bacillariophyceae) is conspicuously evident. The pattern of species richness per site is highly variable (Figure 4A), presumably due to pronounced habitat variability (see previous and next sections). The highest numbers of taxa and percentages of the total flora are found on the exposed open coast at Otter Cliffs (54 and 48%) and Seawall (60 and 53%); the lowest numbers are recorded at several sheltered sites, including Hadley Point (7 and 6.2%) Somesville (6 and 5.3%), Seal Cove (6 and 5.3%), and Bartlett Narrows (6 and 5.3%). The mean number of taxa per site is relatively low (24.5 ± 16.2): green algae 7.0 ± 5.0, brown algae 9.0 ± 4.9, and red algae 8.1 ± 7.1.

As shown in Figure 4B, the pattern of mean number of shared taxa "mimics" species richness, while the values for mean percent similarity exhibit a broader, more uniform pattern (Figure 4C). The overall mean richness values for the 28 present sites are relatively low, being 9.5 ± 5.1 taxa and 36.8 ± 7.6%. Seawall, the site with the highest number of taxa (60), has the highest number of shared taxa (19.0 ± 14.4) and a relatively high percent similarity pattern of 42.0 ± 24.6%. Otter Cliffs, the next most diverse site (54 taxa), has a lower number of shared taxa (15.5 ± 12.7) and percent similarity (39.0 ± 24.0%). By contrast, the four sites with the most reduced floras exhibit the following patterns: (1) Bartlett Narrows, 6 taxa, 4.6 ± 1.7 shared taxa, and 34.0 ± 18.2% similarity; (2) Hadley Point, 7 taxa, 3.0 ± 2.1 shared, and 21.5 ± 20.3% similarity; (3) Seal Cove, 6 taxa, 3.5 ± 1.2 shared, and 28.6 ± 19.3% similarity; and (4) Somesville, 6 taxa, 2.2 ± 1.2 shared, and 18.3 ± 17.6% similarity.

A further comparison of floristic similarities at Otter Cliffs (site 11), Otter Cove (site 13), Seawall (site 22), and Thompson Island (site 1) is given in Figure 5. The values are expressed as percentage of shared taxa with each of the other 27 study sites. Three of these sites were chosen because of concurrent zonation studies (see below), while the fourth (Seawall) had the most diverse flora (Figure 4A). Recalling the clockwise orientation of the sites starting from Thompson Island (Figure 2), the floristic affinities of the exposed site at Seawall show the following spatial pattern: (1) moderately high similarities (66%) with nearby Bass Harbor Head Light (site 23); (2) low-moderate similarities (13–31%) between Bass Harbor (site 24) and Hulls Cove (site 4); (3) maximum affinities with Great Head (site 7, 71%), Thunder Hole (site 10, 73%), and Otter Point (site 12, 77%); and (4) lowest overall similarities with Somesville (site 19, 10%). By contrast, Otter Cliffs has its maximum similarities to nearby Schooner Head (site 6, 67%), Thunder Hole (site 10, 63%), and Otter Point (site 12, 72%), and its lowest affinities with Somesville (site 19, 11%) and those sites between Thompson Island and Hulls Cove (sites 1–4, 7–13%). Otter Cove's affinities are analogous to Otter Cliffs, except for its greater similarities between sites 1–4 (Thompson Island to Hulls Cove, 14–27%) and sites 16–28 (Bracy Cove to Indian Point, 17–64%). Thompson Island shows a very skewed pattern, with maximum affinities at sites 20 (Somesville at Rt. 102, 48%), 25 (Seal Cove, 53%), and 28 (Indian Point, 61%).

Figure 6 outlines the frequency distribution patterns of the 113 individual taxa recorded from the 28 present study sites on Mount Desert Island. Twenty-three species (5 green, 8 brown, and 10 red algae) are restricted to a single site (3.6% occurrence), while 34 others (10 green, 9 brown, and 15 red algae) occur at two or three sites (7.1–10.7% occurrence). Only three taxa occurred at >21 of the 28 sites (Figure 7; Table 1), namely, *Ascophyllum nodosum* (93%), *Fucus vesiculosus* (86%), and *Chondrus crispus* (79%). The other common species are *Scytosiphon simplicissimus* (71%), *Urospora penicilliformis* (64%), *Monostroma grevillei* (61%), *Petalonia fascia* (61%), *Enteromorpha intestinalis* (54%), *Pilayella littoralis* (54%), *Mastocarpus stellatus* (54%), *Berkeleya rutilans* (50%), *Fucus spiralis* (50%), *Ralfsia verrucosa* (50%), and *Polysiphonia lanosa* (50%).

Historical floristic comparisons. As shown in Figure 8A, 121 seaweeds have been previously recorded for Mount Desert (49 Rhodophyceae, 40 Phaeophyceae, and 32 Chlorophyceae) compared with 113 taxa from recent sampling, i.e., 43 Rhodophyceae, 37 Phaeophyceae, and 33 Chlorophyceae. This represents a total of 146 taxa when the two lists are combined, including 41 Chlorophyceae, 50 Phaeophyceae, and 55 Rhodophyceae. In addition, a common diatom *Berkeleya rutilans* is listed in Table 1. Eighty-eight of these taxa are found in both historical and present collections (i.e., 37 red, 27 brown, and 24 green algae). Thus, a comparison of Mount Desert's total flora shows an approximate equality of species numbers (121 vs. 113) and a relatively high percent similarity (75.2%). Similar comparisons of three individual sites (Figure 8B–D) show the following patterns: (1) Otter Cliffs, 54 current taxa, 43 historical, 64 combined total, and a 68% similarity; (2) Seal Harbor, 41 current taxa, 82 historical, 97 combined total, and a 43% similarity; and (3) the Seawall-Southwest Harbor area, 60 current taxa, 63 historical, 90 combined total, and a 54% similarity.

Present-day zonation patterns. As shown in Figure 9 and Table 2, several conspicuous differences in zonation patterns are evident when the Mount Desert sites of Otter Cliffs, Otter Cove, and Thompson Island are compared with previously published records. The biological zones at Otter Cliffs (Figure 3A) are the most expansive (>5.7 m) due to extreme wave exposure, followed by the exposed Bald Head Cliff site (4.8 m), the semi-exposed Jaffrey Point (3.4 m), and the more sheltered Otter Cove (3.2 m) and Thompson Island sites (3.5 m). Thus, the biological zones exceed mean tidal amplitudes at Otter Cliffs (4.6 m), Bald Head Cliff (2.7 m), and Jaffrey Point (2.7 m), while they are less at Otter Cove (4.6 m) and Thompson Island (5.0 m). As shown in Table 2, the freshwater green alga *Mougeotia* and the terrestrial-marine red alga *Porphyridium purpureum* were recorded by Johnson and Skutch (1928c) within the extreme spray-mist zone at Otter Cliffs, extending from 4.3 m–9.2 m (Figure 9A; Table 2); neither of these taxa were found at the other study sites.

Pronounced localized differences in zonation patterns are evident at Otter Cliffs (Figure 9B–D). That is, the exposed outer rocks have a very circumscribed zonation (see below) and a reduced number of species compared with the adjacent semi-exposed cliff. A composite of the two major habitats at Otter Cliffs (Figure 9B) tends to show a more "typical" zonation pattern, similar to Jaffrey Point (Figure 9G), with species richness increasing from top to bottom and a conspicuous stratification of colors. Green algae dominate the upper shoreline, reds are most conspicuous in the lower shore and browns exhibit an intermediate pattern. Many species exhibit disjunct vertical distributions, extending higher within than outside of tide pools (Table 2). A pattern of decreasing species richness with enhanced shelter is also evident on Mount Desert Island, from Otter Cliffs (Figure 9B–D), to Otter Cove (Figure 9E) and Thompson Island (Figure 9F). Of the three groups of seaweeds, the green algae showed the

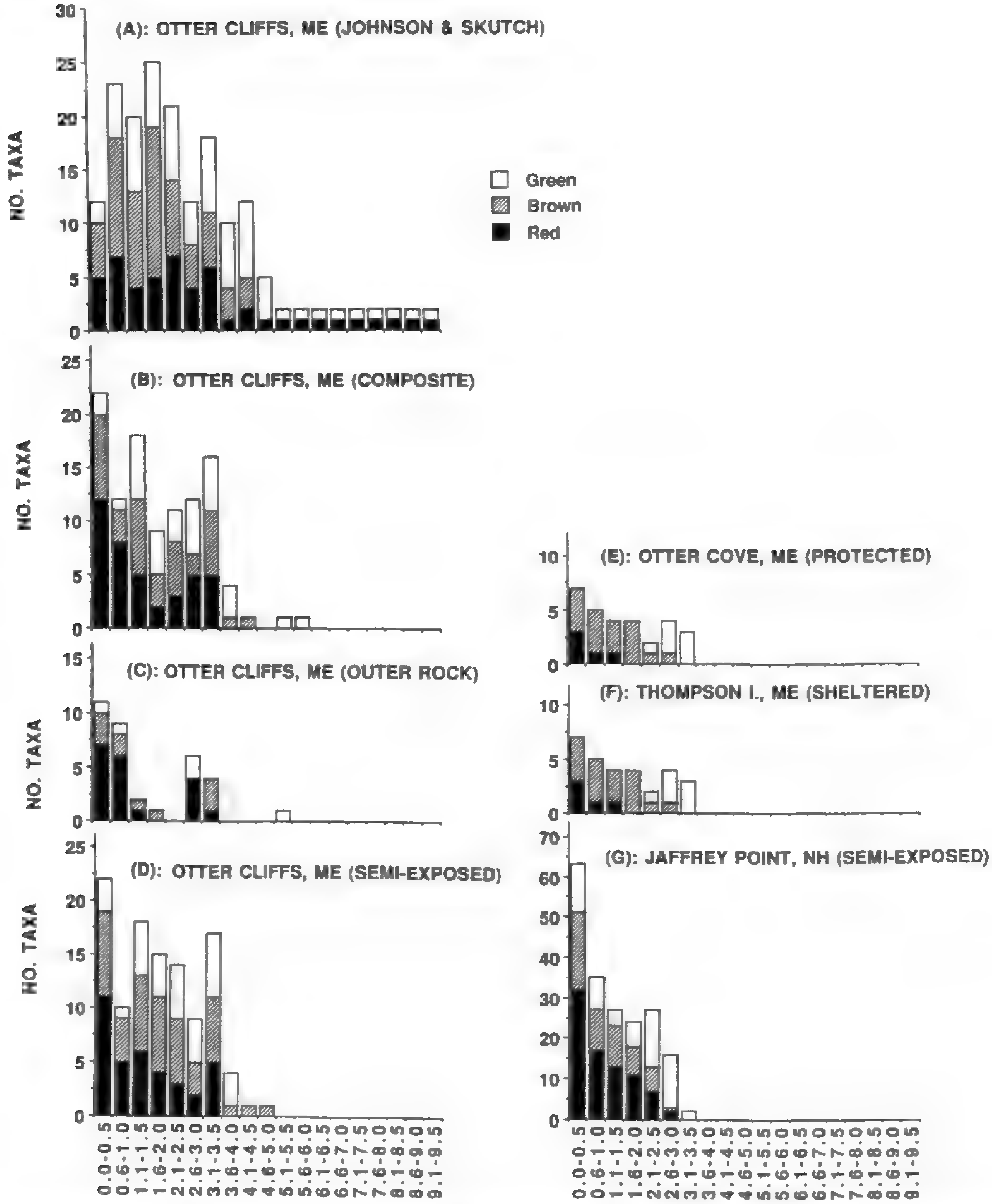

Figure 9. The number of seaweed taxa (green, brown, and red) occurring at 0.5 m intervals from the upper to the lower intertidal zone at six sites in Maine (A–F) and one (G) in New Hampshire: (A) Otter Cliffs (from Johnson and Skutch 1928a); (B) Otter Cliffs, composite of C and D below; (C) Otter Cliffs, outer rocks; (D) Otter Cliffs, inner semi-exposed rocks; (E) Otter Cove, protected open coast; (F) Thompson Island, sheltered bay; (G) Jaffrey Point, semi-exposed open coast.

most conspicuous decrease in species richness (not biomass) with increasing shelter.

A number of unique features are evident when the four major zones (maritime, splash, intertidal, subtidal) on Mount Desert are compared (Table 2). The maritime zone, or the area subjected to salt spray above the highest tides, is absent from the exposed rocks at Otter Cliffs that only reach 5.7 m above MLW. It is well developed, however, on the adjacent cliffs (+9.2 to +15.2 m). Within this zone several lichens (*Caloplaca*, *Leonia*, *Physia*, *Ramilina*, *Verrucaria*, and *Xanthoria*), blue green algae (*Calothrix* and *Oscillatoria*), and seed plants (*Abies balsamea*, *Empetrum nigrum*, *Juniperus horizontalis*, *J. communis* var. *depressa*, *Picea glauca*, and *Plantago oliganthos*) occur. Many seed plants exhibit extensive wind/salt damage. At Otter Cove (Figure 3B) and Thompson Island (Figure 3C) the maritime zone approximates mean tidal limits, extending to +4.6 and +5.0 m, respectively. The two most conspicuous trees at these sites, *A. balsamea* and *P. glauca* show little wind/salt damage. The splash zone, or the area affected by wave action above high tide, exhibits pronounced spatial differences. It extends to the top of the outer rocks at Otter Cliffs (+5.7 m) where only a few localized patches of the guanotrophic green alga *Prasiola stipitata* occur (Table 2). On the adjacent semi-exposed cliff, it extends to about +9.2 m, with the marine lichen *Verrucaria* spp. and various blue green algae (*Calothrix* and *Oscillatoria*) forming extensive greenish-blackish crusts. A splash zone is absent at Otter Cove and Thompson Island, and their biological zones do not exceed ambient tidal extremes (see above).

The intertidal zone, or the region regularly covered and uncovered by tides, can be divided into three major subzones: (1) an upper barnacle zone dominated by *Semibalanus balanoides*; (2) a mid-shore brown algal zone with *Ascophyllum nodosum* and *Fucus* spp.; and (3) a lower red algal zone with *Chondrus crispus* and *Mastocarpus stellatus*. The upper intertidal at the exposed Otter Cliffs rocks (ca. +3.0 to +4.6 m) is dominated by *S. balanoides*, while several disjunct taxa occur within high tide pools (*Ulva lactuca*, *Ulvaria obscura*, *A. nodosum*, *Fucus distichus* ssp. *distichus*, "*Ralfsia clavata*," *Ahnfeltia plicata*, *Chondrus crispus*, *Clathromorphum circumscriptum*, *Devaleraea ramentacea*, *Hildenbrandia rubra*, and *Mytilus edulis*). The mid-intertidal (ca +1.6 to +2.9 m) only has a few stunted plants of *F. distichus* ssp. *edentatus*, plus *S. balanoides*, while the low intertidal (0.0 to ca +1.5 m) contains many of the same disjunct tide pool taxa, in addition to *Alaria esculenta*, *Elachista fucicola*, *M. stellatus*, *Palmaria palmata*, "*Petrocelis cruenta*," *Polysiphonia stricta*, *Porphyra umbilicalis*, *M. edulis* and *S. balanoides*. The semi-exposed habitat at Otter Cliffs contains a greater variety of organisms than the outer highly exposed rocks (Figure 9C, D), with *S. balanoides* dominating the upper shore (to +3.5 m), *A. nodosum* and *F. vesiculosus* the mid-intertidal (to +2.8 m), and several species in the lower intertidal (*C. crispus*, *M. stellatus*, *P. palmata*, *U. lactuca*, and *M. edulis*). The intertidal zone at Otter Cove is primarily dominated by *S. balanoides*, *A. nodosum*, *F. vesiculosus*, *C. crispus*, and *M. edulis*; epiphytic (*Pilayella littoralis*) and hemiparasitic species (*Polysiphonia lanosa*) are abundant. Analogous zones at Thompson Island are readily differentiated, with *Fucus spiralis* extending from +2.4 to +3.5 m, *A. nodosum* from +0.2 to +2.9 m, and *F. vesiculosus* from 0.0 to +0.8 m.

The upper subtidal zone, or fringe region just below mean low water (MLW), shows pronounced differences in species composition and abundance (Table 2). For example, at the exposed Otter Cliffs, this zone is dominated by dense patches of *Semibalanus balanoides* and *Mytilus edulis*; wave-damaged *Alaria esculenta* and many red and green algae are also evident. *Fucus distichus* ssp. *edentatus* marks the upper subtidal zone at the adjacent semi-exposed cliffs. Several kelps (*A. esculenta*, *Laminaria digitata*, and *L. saccharina*), green algae (*Spongomorpha spinescens* and *Ulva lactuca*), and red algae (*Ceramium nodulosum*, *Clathromorphum circumscriptum*, *Devaleraea ramentacea*, and "*Petrocelis cruenta*") are also present. The shallow subtidal at Otter Cove has dense populations of *Mastocarpus stellatus*, *U. lactuca*, and *L. saccharina*, as well as the crustose algae *C. circumscriptum*, "*P. cruenta*," and *Pseudolithoderma extensum*. Somewhat deeper, *Strongylocentrotus droebachiensis* forms extensive "urchin barrens" in which only residual populations of *Agarum clathratum* are evident on a "pavement" of the pink crustose coralline alga *C. circumscriptum*. Thompson Island has a very limited subtidal flora, and most plants (*Dumontia contorta*, *Polysiphonia flexicaulis*, *Hildenbrandia rubra*, and *Ralfsia verrucosa*) occur on scattered granitic boulders and pebbles.

Figure 10 illustrates the upper distributional limits of seven conspicuous seaweeds at five sites on Mount Desert Island (Otter Cliffs: a composite, the exposed outer rocks, and the semi-exposed cliffs; Otter Cove, and Thompson Island), plus Bald Head

Cliff, Maine, and Jaffrey Point, New Hampshire. *Ascophyllum nodosum* shows a fairly uniform distribution, being most circumscribed at Otter Cove and Jaffrey Point. *Fucus vesiculosus* exhibits a conspicuous attrition with enhanced shelter between the Otter Cliffs composite site and Thompson Island and a moderate resurgence at Bald Head and Jaffrey Point. *Mastocarpus stellatus* and *Chondrus crispus* are highly reduced at the most exposed sites, the outer rocks of the highly exposed Otter Cliffs and those of the more protected Otter Cove. The former species has an erratic distribution, while the latter species shows a southerly enhancement. *Clathromorphum circumscriptum* exhibits a more northern pattern than *C. crispus* and is most prevalent in the composite of Otter Cliffs and their highly exposed outer rocks. *Palmaria palmata* is most common at the composite of Otter Cliffs, it dips on the exposed outer rocks, and is lowest at the semi-exposed Jaffrey Point. *Devaleraea ramentacea* is relatively uniform at all sites except at Jaffrey Point, where it is reduced.

The upper and lower distributional limits of *Verrucaria* spp., *Urospora penicilliformis*, and *Blidingia minima* are illustrated in Figure 11. *Verrucaria* shows its maximum upward expansion at the semi-exposed rocks of Otter Cliffs and the more protected coast of Otter Cove with analogous lower distributional limits, except for the latter site and Thompson Island. *Urospora* is most expansive at the composite of Otter Cliffs and shows a clinal decrease/compression at the other five sites. *Blidingia* shows a maximum upper distribution at the same site; minimum limits are seen at Otter Cove and Jaffrey Point. Its lower distribution is somewhat erratic, with maximum and minimum levels in the composite and semi-exposed areas of Otter Cliffs, respectively.

Historical zonation comparisons. The use of Johnson and Skutch's benchmark, which was established in 1923 at Otter Cliffs, has insured that the present elevational measurements are directly comparable. Based upon these comparisons, 13 of the 32 shared taxa (4 green, 4 brown, and 5 red) show a conspicuous reduction (0.5 to 2.0 m) in their upper distributional limit (Table 3). Three species also show a drop in their lower distributional limits: *Blidingia minima* (3.7 m vs. 1.8 m), *Fucus vesiculosus* (1.5 m vs. 0.1 m) and *Porphyra umbilicalis* (0.6 m vs. 0.0 m). None of the 32 shared taxa shows a significant upward expansion of its zone (>0.2 m).

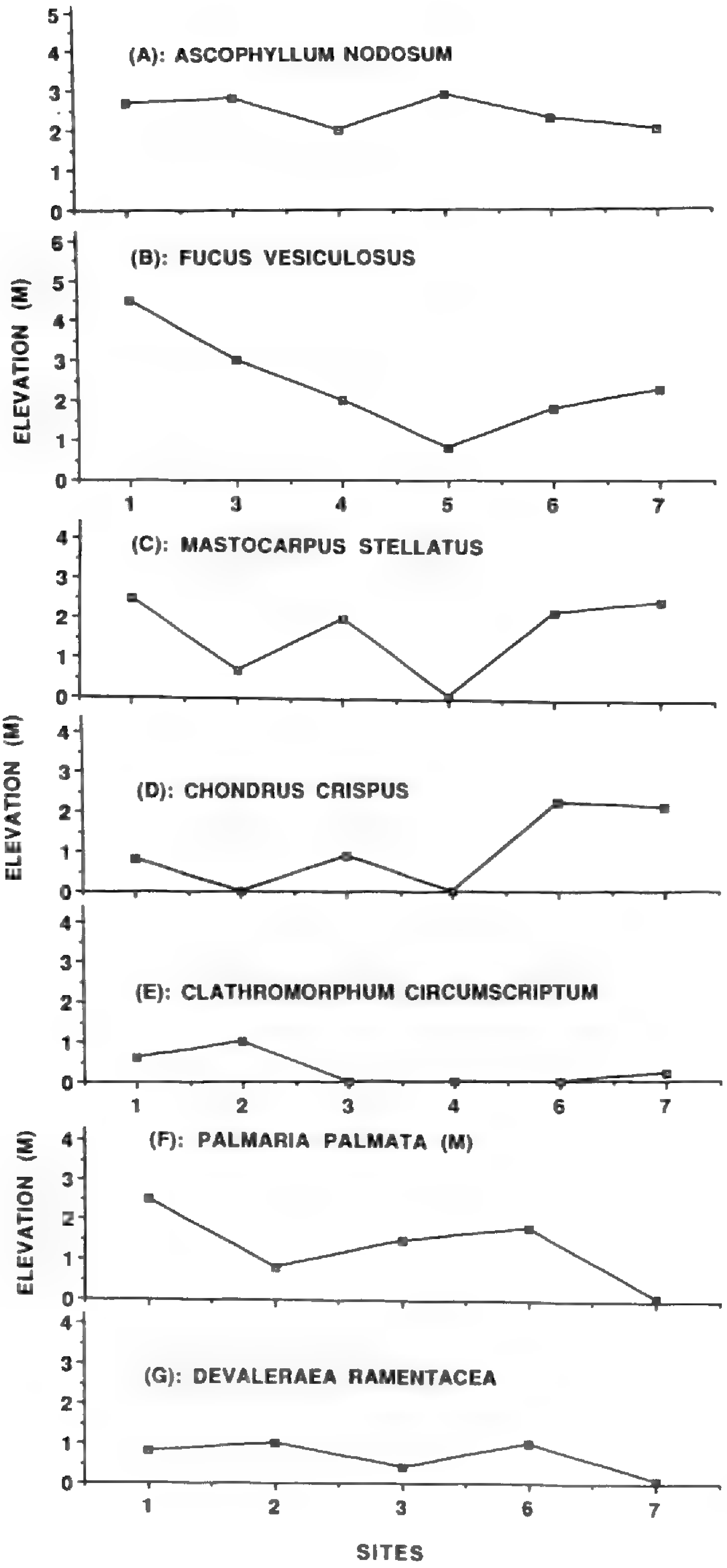

Figure 10. Upper distributional limits of non-tide pool populations of *Ascophyllum nodosum* (A), *Fucus vesiculosus* (B), *Mastocarpus stellatus* (C), *Chondrus crispus* (D), *Clathromorphum circumscriptum* (E), *Palmaria palmata* (F), and *Devaleraea ramentacea* (G) at seven sites. The sites are: (1) Otter Cliffs (from Johnson and Skutch 1928a); (2) outer rocks at Otter Cliffs;

DISCUSSION

Based upon historical and recent collections, the macroalgal flora on Mount Desert Island, Maine, is composed of 145 taxa, which exceeds insular floras within nearby Penobscot Bay and at other northwest Atlantic sites (Mathieson and Penniman 1986; Mathieson et al. 1996). When comparing historical and recent collections at three individual sites on Mount Desert, the lowest percent similarity occurred at Seal Harbor, an embayment having intense human activity, while other sites showed only small changes. Zonation studies revealed altered vertical patterns and a reduction in species diversity with increasing exposure, with these patterns being similar to those reported for the Bay of Fundy (Morton 1991) and rocky shores in general (Dawes 1998; Lewis 1964; Lobban and Harrison 1994; Lüning 1990; Stephenson and Stephenson 1972). A significant decline in elevation for 13 intertidal seaweeds at Otter Cliffs also occurred during the 74 year period, with no upward expansion for 20 additional species.

Three major present-day seaweed floristic patterns are evident when comparing percent similarities at Mount Desert Island: (1) the values for individual sites are variable, presumably because of pronounced habitat differences; (2) the mean value for the 28 present study sites is quite low ($\bar{x}$ = 36.8 ± 7.6%); (3) the latter value is much lower than similarity values for multiple northwest Atlantic sites (ca. 51.0–92.0%, $\bar{x}$ = 72.3% ± 6.0%) from Campobello Island, New Brunswick, to Penikese Island, Buzzards Bay, Massachusetts (Mathieson et al. 1996). Thus, there are strong contrasts between intra- and interisland percent similarity patterns, which are important in assessing possible anthropogenic impacts (Anonymous 1992, 1995; Greene et al. 1992) as well as evaluating theoretical considerations regarding island biogeography (Mathieson and Penniman 1986). Further, the frequency distribution patterns shown in Figure 6 show that many taxa are

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(3) inner semi-exposed rocks at Otter Cliffs; (4) Otter Cove; (5) Thompson Island, sheltered bay; (6) exposed rocks of Bald Head (Femino and Mathieson 1980); and (7) semi-exposed Jaffrey Point (Mathieson et al. 1981). Note that five of the species were not found at all seven sites including: *A. nodosum* and *F. vesiculosus* (site 2), *M. stellatus*, *C. crispus*, and *C. circumscriptum* (site 5), and *P. palmata* and *D. ramentacea* (site 4 and 5).

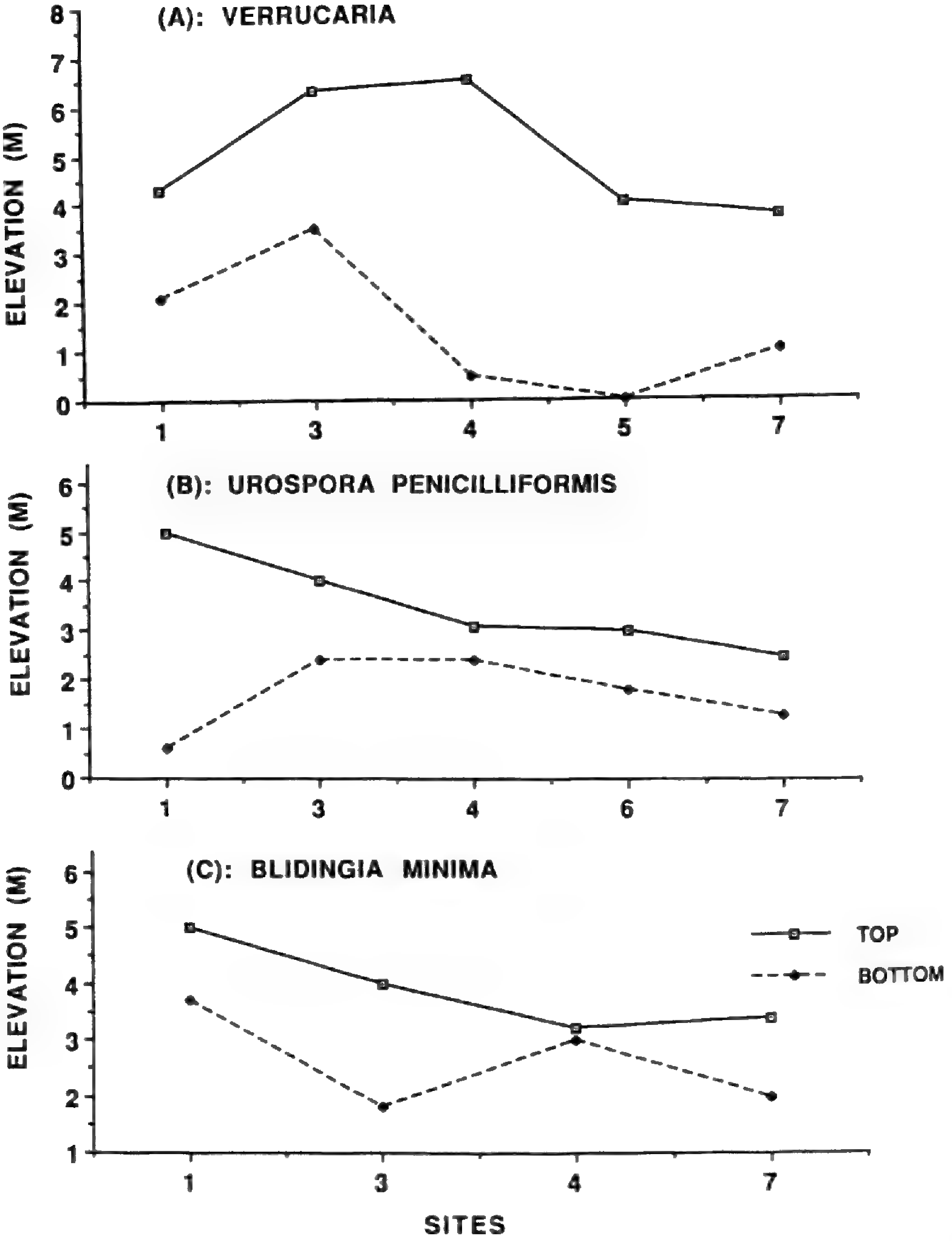

Figure 11. Upper and lower vertical distributions of non-tide pool populations of *Verrucaria* spp. (A), *Urospora penicilliformis* (B), and *Blidingia minima* (C), with site delineations as in Figure 10. The species were not collected at site 2, *Verrucaria* spp. were missing from site 6, *U. penicilliformis* from site 5, and *B. minima* from sites 5 and 6.

Table 3. Difference in upper distributional limits of intertidal seaweeds at Otter Cliffs, Maine, determined from 1923–1927 (Johnson and Skutch 1928a) and 1996. Data for floristic affinities and southern distributional limits are based upon Schneider and Searles (1991), South and Tittley (1986), and Taylor (1957). Key to symbols: Affinities: C = cosmopolitan; N = northern; Southern limits: CT = Connecticut; MA = Massachusetts; NC = North Carolina; NJ = New Jersey; VA = Virginia; * = species showing drop in lower distributional limit.

Species	1928	1996	Difference	Affinities	Limits
CHLOROPHYCEAE					
*Blidingia minima**	5.0 m	4.0 m	−1.0	C	VA
"Codiolum pusillum"	4.5 m	4.0 m	−0.5	N	MA
Spongomorpha arcta	2.5 m	0.5 m	−2.0	C	NJ
Urospora penicilliformis	5.0 m	4.0 m	−1.0	C	VA
PHAEOPHYCEAE					
Elachista fucicola	2.5 m	1.5 m	−1.0	C	CT
Fucus distichus ssp. *edentatus*	2.5 m	2.0 m	−0.5	N	MA
*Fucus vesiculosus**	4.5 m	3.0 m	−1.5	C	NC
Laminaria digitata	0.5 m	0.0 m	−0.5	C	CT
RHODOPHYCEAE					
Mastocarpus stellatus	2.5 m	2.0 m	−0.5	C	CT
Palmaria palmata	2.5 m	1.5 m	−1.0	C	NJ
Polysiphonia lanosa	3.0 m	2.5 m	−0.5	C	NJ
Polysiphonia stricta	2.5 m	1.0 m	−1.5	C	NC
*Porphyra umbilicalis**	3.5 m	3.0 m	−0.5	C	VA

cosmopolitan, occurring in diverse open coastal and estuarine sites in New England (Mathieson and Hehre 1986; Mathieson and Penniman 1991).

Several present-day comparisons of Mount Desert and other northwest Atlantic North American insular floras also can be made. Foremost, Mount Desert's macroalgal flora (145 taxa) exceeds the most floristically diverse, smaller islands (Mathieson and Penniman 1986) of Smuttynose Island, Maine (136 taxa), and Penikese Island, Massachusetts (131 taxa); at the same time, its species diversity is considerably less than Newfoundland (ca. 254 taxa), the largest island within this same geography (South 1983; South and Hooper 1980). A comparison of nine smaller islands within contiguous Penobscot Bay (Figure 1) shows a range of 4–65 taxa/island ($\bar{x}$ = 30.8 ± 23.0) and 97 total taxa (Mathieson et al. 1996). Further, Mount Desert's flora exceeds the insular floras of Penobscot Bay, both individually and collectively. In a broader context, Mount Desert's flora is relatively diverse compared with contiguous coastal embayments: (1) 159 taxa for Passamaquoddy Bay, New Brunswick, Canada (Tittley et al. 1987); (2) 139 taxa for Penobscot Bay as a whole, including insular and nearshore sites (Mathieson et al. 1996); (3) ca. 194 taxa for Casco Bay, Maine (Collins 1911; Farlow 1881; Mathieson and Hehre, unpubl. data). Thus, macroalgal diversity can be related to island size, which in turn is correlated with habitat complexity (positively) and anthropogenic impacts (negatively).

With respect to historical floristic comparisons, Otter Cliffs shows an apparent "enhancement" of species richness, Seal Harbor exhibits a conspicuous reduction and Seawall-Southwest Harbor shows approximate equality. The inconsistent patterns might result from several factors: incomplete characterization of Otter Cliffs (Johnson and Skutch 1928a, b, c), temporal variability of the floras (Harris et al. 1998), or anthropogenic effects (e.g., Seal Harbor). Thus, different factors may be important in determining individual patterns. Two of the most conspicuous factors are habitat diversity and frequency of collections. For example, a comparison of the seaweed flora of the semi-exposed Jaffrey Point, New Hampshire, site showed a pattern of maximum species richness (see Figure 9G), presumably because of its "intermediate" environment (Connell 1979), plus the fact that detailed seasonal and spatial collections were made (Mathieson et al. 1981, 1991).

As shown in Table 3, eleven of the thirteen species with altered historical zonation patterns are cosmopolitan, being widely distributed north and south of Cape Cod, Massachusetts. The other two taxa ("*Codiolum pusillum*" and *Fucus distichus* ssp. *edentatus*) are more common north than south of the Cape (South and Tittley 1986; Taylor 1957). It should be emphasized that seaweed zonation patterns can be influenced by abiotic factors such as wave activity (Figures 9–11), as well as varying climatic conditions. For example, in a study of intertidal invertebrates at Monterey Bay, California, Barry et al. (1995) found that 8 out of 9 "southern" taxa showed an increase in abundance between 1931 and 1994. By contrast, 5 of 8 "northern" species decreased in abundance during the same period. Barry et al. suggest that the basis for these changes could be an increase in air and water temperature. In the Gulf of Maine, Harris et al. (1998) reported that several "southern" subtidal invertebrates expanded their distribution between 1979 and 1994, presumably due to an increase in mean seawater temperatures of approximately 1°C during this same period. Introduced taxa included the southern sea star *Asterias forbesi*, the tunicate *Diplosoma* sp., and the exotic green alga *Codium fragile* ssp. *tomentosoides*. The downward shift in elevation of 13 intertidal seaweeds at Otter Cliffs may be caused, in part, by the general warming trend noted in the Gulf of Maine (Harris et al. 1998). However there was no expansion of more "southern" intertidal taxa as reported by Barry et al. (1995). Another possible factor influencing intertidal distribution is increased atmospheric ozone levels. Indeed, high levels of this pollutant have been monitored at Acadia National Park in the 1980s and extensive damage to terrestrial plants, including spreading dogbane, has occurred due to ozone injury (Eckert et al. 1994, 1997).

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APPENDIX

HISTORICAL AND RECENT COLLECTIONS FROM MOUNT DESERT, MAINE, AND ADJACENT CRANBERRY ISLES, INCLUDING SITES, DATES, AND NAMES OF COLLECTORS.

Site:

1. Thompson Island, Mount Desert Narrows, Bar Harbor (Recent: 11/16/1996)
2. Old House Cove, Mount Desert Narrows, Bar Harbor (Recent: 10/6/1994)
3. Hadley Point, Mount Desert Narrows, Bar Harbor (Recent: 4/16/1995)
4. Hulls Cove, Frenchman Bay, Bar Harbor (Recent: 4/3/1995)
5. Town pier, Bar Harbor (Recent: 4/14/1967, 4/14/1968, 1/14/1983, 4/3/1995)

5a. Bar Harbor (Historical: FSC: 7/1896; HWG & GHG: 10/1949; MZ: 8/18/1966)

6. Schooner Head/Anemone Cave area, Bar Harbor (Recent: 4/16/1995, 2/22/1996, 5/5/1996)
7. Great Head, Bar Harbor (Recent: 4/3/1995)
8. Sand Beach, Bar Harbor (Recent: 4/16/1995, 2/22/1996)
9. Old Soaker, Bar Harbor (Recent: 2/22/1996)
10. Thunder Hole, Bar Harbor (Recent: 4/15/1955, 9/25/1981, 2/22/1996, 5/5/1996)
11. Otter Cliffs, Bar Harbor (Historical: FSC: 7/12/1900, 7/17/1900, 7/20/1900; DSJ: 6/1927, 6/5/1927, 6/23/1927, 7/1927, 7/9/1927; DSJ & AFS: 1928 (Msc.); Schramm: 1941; Recent: 9/25/1981, 8/23/1994, 10/25/1996)
12. Otter Point, Bar Harbor (Recent: 4/13/1967, 4/13/1968, 8/25/1994, 4/16/1995, 5/5/1996)
13. Otter Cove, Bar Harbor (Recent: 4/25/1996, 8/23/1996, 10/25/1996)

13a. Otter Creek, Mount Desert (Historical: FSC: 7/12/1900, 7/17/1900, 7/20/1900)

14. Western Point, near Black Woods Campground, Mount Desert (Recent: 5/15/1970, 5/15/1971, 3/25/1995, 2/22/1996)

14a. Hunter's Beach, near Ingraham Point, Mount Desert (Historical: FSC: 7/11/1900, 7/11/1902)

15. Seal Harbor, near Crowninshield Point, Mount Desert (Historical: LRB: 1890; FSC: 7/24/1889, 7/1890, 7/2/1890, 7/22/1890, 8/8/1890, 8/11/1890, 1894 (Msc.), 7/1897, 6/17/1899, 7/1899, 7/15–7/17/1899, 7/14/1900; IH: 8/17/1889; EWR: 8/1888; Recent: 3/25/1995, 4/15/1995, 5/5/1995, 2/22/1996, 9/29/1996)
16. Bracy Cove, Mount Desert (Historical: FSC: 7/22/1889, 7/20/1890; IH: 8/11/1890; Recent: 3/25/1996, 5/5/1996)
17. Northeast Harbor, Mount Desert (Historical: HdR: 8/1903; Recent: 3/25/1995, 2/22/1996)

17a. Little Cranberry Isle, Cranberry Isles (Historical: FSC: 1894 (Msc.), 7/20/1890, 7/21/1890, 7/15/1899, 7/16/1899; JHR: 8/6/1889)

18. Somes Sound, off of Sargent Drive & opposite Acadia Mountain/Norumbega Mountain Viewpoint, Mount Desert (Recent: 3/25/1995)

19. Somesville, near junction of Routes 102 & 198, Mount Desert (Historical: FSC 7/24/1889; WJO 9/25/1912; Recent: 8/24/1994)
20. Somesville, @ Rt. 102 & a tidal stream, Mount Desert (Recent: 3/25/1995)
21. Clark Point near U.S. Coast Guard Facility, Southwest Harbor (Historical: AJB and ETM: 7/26/1952; FSC: 7/24/1889, 7/1897, 7/17/1897; IH: 8/2/1889, 8/12/1889, 8/15/1889, 8/17/1889, 8/2/1890, 8/3/1890, 8/6–8/1890, 8/10/1890; Recent: 3/25/1995)
21a. Greening Island, Southwest Harbor (Historical: IH: 8/7/1890)
21b. Near Wonderland Trail, Southwest Harbor (Historical: AFH: 8/11/1889)
22. Seawall, across from Seawall Campground, Southwest Harbor (Historical: FSC: 7/1897, 7/18/1897; IH: 1883, 7/17/1887, 8/1889, 8/8/1889, 8/10/1889, 8/12/1889, 8/15/1889, 8/17/1889, 8/8/1890, 8/12/1890, 7/1897, 7/18/1897, 3/19/1903; DSJ: 7/1927, 7/9/1927; WRT: 9/5/1920, 8/26/1970; Recent: 8/23/1994, 8/24/1994, 3/25/1995, 4/16/1995, 2/23/1996)
23. Bass Harbor Head Light, Tremont (Recent: 3/25/1995, 2/23/1996)
24. Bass Harbor, @ culvert on Rt. 102, Tremont (Recent: 8/24/1994)
25. Seal Cove, Blue Hill Bay, Tremont (Recent: 4/16/1995)
26. Pretty Marsh Harbor, @ Indian Point Road, Mount Desert (Recent: 4/18/1995)
27. Bartlett Narrows boat ramp, off of Indian Point Road, Mount Desert (Recent: 4/18/1995)
28. Indian Point @ Blagden Preserve, Western Bay, Bar Harbor (Recent: 4/18/1995)
29. Recorded from Mount Desert Island with no specific location (Historical: FSC: 7/1900)

Historical Collectors: AJB: Albert J. Bernatowitz; LRB: L. R. Boggs; FSC: Frank S. Collins; GHG: Gilbert H. Goff; HWG: Helen W. Goff; AFH: Albert F. Hill; IH: Isaac Holden; DSJ: Duncan S. Johnson; ETM: Edward T. Moul; WJO: Winthrop J. Osterhout; EWR: Elisa W. Rand; JHR: John H. Redfield; HdR: H. de Roasloff; Schramm; AFS: Alexander F. Skutch; WRT: William R. Taylor; MZ: Martin Zimmerman.

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THE SEDGES (CYPERACEAE) OF BARBADOS

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ABSTRACT. After decades of neglect, the sedge flora of Barbados was reappraised, beginning with intensive collections made across the island. Twenty-eight species of Cyperaceae from the genera *Abildgaardia*, *Cyperus* (including *Mariscus*), *Eleocharis*, *Fimbristylis*, *Kyllinga*, *Pycreus*, *Rhynchospora*, *Scleria*, and *Torulinium* are described and illustrated with photographs. Keys are provided to all of the species, as well. Five species are added to the flora of Barbados. Species previously recorded but not found recently are noted.

Key Words: *Abildgaardia*, Antilles, Barbados, Cyperaceae, *Cyperus*, *Eleocharis*, *Fimbristylis*, flora, *Kyllinga*, *Mariscus*, *Pycreus*, *Rhynchospora*, *Scleria*, sedges, West Indies

Barbados is the easternmost island of the Lesser Antilles in the West Indies, located just north of 13 degrees N lat. and a little west of 59 degrees W long. It is tropical with a pronounced wet season July through November and a pronounced dry season January through April. The average annual rainfall of 1000–2000 mm is distributed unevenly across the landmass. Differing geologically from its neighbors, Barbados is almost entirely coral-derived and dominated by alkaline clays and coral rock with small areas of exposed sandstone. The topography is rolling and sharply tiered in places, with the highest elevation about 340 m. Due to the island's small size (ca. 18 km × 26 km), the entire landmass is "coastal" and exposed to salty winds.

The original flora is virtually gone, and the biota is a mix from various sources reflecting centuries of human activity. Barbados was inhabited by Native Americans before the arrival of Europeans in the early 1600s. For centuries most of the area has been covered with cultivated sugarcane, with pastures dominated by imported grasses, and with disturbed scrubby areas. Only a small number of tiny forest remnants approximate the original vegetation, most notably Turner's Hall Woods in St. Andrew Parish and the Hackleton's Cliff area, including Foster Hall Woods, in St. Joseph and St. John Parishes. Miles of sharp gullies in the limestone house partially wild vegetation, though these places are not rich in sedges.

Throughout Barbados are minor freshwater streams and seeps, well provided with sedges. The island is ringed with beaches interspersed with stretches of rugged, rocky coastline. Behind the beaches are often sandy, scrubby woods, or dunes, or brackish pools. Most notable of these is the Chancery Lane "Swamp" (brackish marsh) on the southeastern coast in Christ Church Parish. Few significant true swamps remain, although there are patches of woody vegetation on wet coastal sites.

Of these, Graeme Hall Swamp on the south coast in Christ Church Parish is a vegetatively diverse mangrove swamp, marsh, and scrubland with the best array of sedges in Barbados. The dominant understory plant is the sedge *Eleocharis mutata*. Scattered throughout much of the swamp, this species covers acres as a nearly monospecific "lawn" on low, wet, marly soil in full sun and in shade. The areas dominated by *E. mutata* were called "Sedge Swamp" association by Gooding (1974). He placed the association in areas of reduced salinity or virtually fresh water behind mangrove swamp. Other members of the Sedge Swamp association occurring in Graeme Hall Swamp are *Abildgaardia ovata*, *Blutaparon vermiculare* (L.) Mears, *E. geniculata*, *Fimbristylis ferruginea*, and *Sporobolus virginicus* (L.) Kunth. Additional sedges found in Graeme Hall Swamp are *Cyperus alopecuroides*, *C. elegans*, *C. ligularis*, *C. planifolius*, *C. rotundus*, *F. cymosa*, *Kyllinga brevifolia*, *Pycreus polystachyos*, *Scleria melaleuca*, and *Torulinium odoratum*. *Cyperus laevigatus* was collected there in the past but has not been encountered recently, even in an intensive floristic inventory of Graeme Hall Swamp carried out in 1996 and 1997 by Rogers and Dr. Sean Carrington of the University of the West Indies. In short, a single small site on the order of 80 acres provides habitat for most of the sedges encountered in Barbados. This is of some significance, since the site is the new home of a sewage treatment plant and is under development as an "ecotourism" attraction.

Sedges in Barbados have been ignored in recent years. The most up-to-date treatments are in the *Flora of the Lesser Antilles* (Koyama 1979) and in the *Flora of Barbados* (Gooding et al. 1965). The *Flora of the Lesser Antilles* is broad in scope, making it especially useful for identifications, overall ranges, and nomenclature. By the same token, the attention to Barbados is minimal, and experience shows the work to be of limited applicability to Barbados. The *Flora of Barbados* treatment is in need of an up-date. It was written with no field work and was based on a limited number of specimens collected largely in the 1930s and 1940s. Conditions have changed; taxonomic concepts and nomenclature have changed; the sedge flora has changed.

The present work lacks the breadth required to provide many taxonomic insights into taxa with the vast distributions characteristic of most of the sedges treated. Taxonomically and nomenclaturally we have, therefore, tended to conform with Koyama except in cases with clear reasons to diverge. As one such case, we were unable to perceive *Mariscus* as a genus apart from *Cyperus*, and adopted the outlook of other taxonomists in treating *Mariscus* as a synonym. We have diverged further from the *Flora of the Lesser Antilles* by following recent authors in treating *Abildgaardia* as distinct from *Fimbristylis*. Some current authors include *Pycreus* and *Torulinium* in *Cyperus*. That we have failed to do so reflects "default" consistency with the *Flora of the Lesser Antilles* rather than taxonomic conviction. We are particularly skeptical of maintaining *Torulinium* apart from *Cyperus*.

At the specific level we have likewise avoided the temptation to judge species boundaries by Barbados experience. An exception, however, was a profound inability to perceive *Cyperus brunneus* as distinct from *C. planifolius*, at least as these are portrayed in the literature. We have encountered sedges consistent with descriptions of both and an array of intermediates. Review of the literature and personal communication with others who have faced this pair engenders a sense that *C. brunneus* is best regarded tentatively as a synonym of *C. planifolius*, pending a comprehensive study that includes the types and materials from the full ranges.

A few sedges have been collected on Barbados but did not turn up in our field work. These are:

Cyperus laevigatus is known in Barbados from three collections, two from brackish sites on the East Coast (1937, 1990) and one from Graeme Hall Swamp (1937). We have repeatedly searched along the East Coast (including the 1990 site) and in Graeme Hall Swamp with no results. The most likely area for the species to be rediscovered is near the mouths of streams in the vicinity of Martin's Bay in St. John Parish.

Cyperus sphacelatus was encountered only once in Barbados, by botanist G. Gooding in August of 1940. We have searched the site and its environs on several occasions. The area where

Gooding found *C. sphacelatus* has been altered since the 1940s, and presently is dominated by cattle farming, although the freshwater stream where the sedge presumably grew is still present though polluted with cattle manure. This stream is the site of the newly encountered *C. alopecuroides.*

Eleocharis macrostachya has been collected just once in the Lesser Antilles, on the East Coast of Barbados in 1904.

Torulinium filiforme was collected once, by S. Carrington in 1989 on the lawn of the Barbados Museum in Bridgetown. We have searched that lawn and the surrounding area without finding this small weedy *Torulinium.*

New sedge records for Barbados turned up by the present work are:

Cyperus alopecuroides has been encountered in three places: one is a stream in St. Philip Parish. The second site is a pond near that stream. The third site is Graeme Hall Swamp. All three places are characterized by standing water and deep, mucky, highly organic, manure-enriched soil smelling of hydrogen sulfide.

Fimbristylis complanata is a pasture (and roadside) weed.

Kyllinga nemoralis is a grassy weed.

Cyperus compressus is known from one locality, a nitrogen-rich weedy lawn adjacent to a stable in Bridgetown.

Cyperus ochraceus has turned up at two spots in Speightstown in St. Peter Parish. One has since been lost to residential development.

MATERIALS AND METHODS

Our general approach has been to search Barbados for sedges, making herbarium collections which we have deposited at BAR and MICH. Most of the field work took place July 1996 to July 1997, with diminished collection activity continuing to March 1998. The determinations were made by us using materials in the herbaria at the University of the West Indies, Barbados (BAR), the University of Florida (FLAS), and the University of Michigan (MICH), by consulting floristic literature, and by consulting other botanists interested in neotropical sedges. Relevant and much-consulted sedge treatments dating from within the last six years are Adams (1992), McVaugh (1993), and Strong (1996). Photographs were taken with a Pentax 35 mm SLR camera using multiple lenses and ASA 100 black and white film. All species descriptions and keys are based entirely on Barbados material in BAR. The key is intended for users other than professional botanists and thus avoids obscure and microscopic characters. Generic descriptions are based heavily on Koyama (1979) though much influenced by other literature and by herbarium work.

Prior to the 1940s, collectors depositing specimens in BAR tended to use *species* numbers rather than the *collection* numbers familiar to all taxonomists. There are many cases where the same species number appears on multiple collections, and there are many cases of a single species number winding up scattered among different species as specimens have been reidentified and as taxonomic concepts have changed. We have cited such old species numbers as though they were collection numbers, finding that confusion is avoided as long as collection dates and localities are cited, also. All collections more recent than the 1940s bear true collection numbers in conformity with modern practice. The collection numbers cited with the photographs apply to collections made at the same sites and from the same species as the photos but not necessarily on the same dates, nor from the same individual plants. When possible, for each species we have added a reference to the *Flora of the Lesser Antilles* ("FLA") and to the *Flora of Barbados* ("Gooding et al., Fl. Barbados").

Potentially confusing terms were applied as follows:

achene—any sedge fruit
bract—foliar organ subtending an inflorescence
culm—inflorescence-bearing stem
order of branching—excludes spikelet axes
pseudolateral—used to describe inflorescence overtopped by a bract that continues the culm axis
rachilla (= rhachilla)—the spikelet axis
ray—first-order branch of an umbellate inflorescence
raylet—second-order branch of an umbellate inflorescence
scale—the small foliar organ subtending an individual flower (referred to as "glume" by some authors)
spike—any spikelet-bearing inflorescence axis
spikelet—the ultimate order of branching, which bears scales and flowers

spikelet length—refers to mature spikelets. Sedge spikelets can elongate dramatically during maturation.

style—branch at the summit of the gynoecium

umbellate—resembling an umbel by having multiple axes diverge spokelike from a single point

KEY TO THE SEDGES OF BARBADOS

1. Plants with cauline leaves; flowers unisexual, the plants monoecious (*Scleria*) .... (2)
 [Note: *Cyperus compressus* sometimes has cauline leaves near the base, but the flowers are perfect.]
 2. Leaves mostly > 5 mm wide; achene with basal swelling (hypogynium) .... 26. *Scleria melaleuca*
 2. Leaves mostly < 2.5 mm wide; achene without basal swelling .... 25. *Scleria lithosperma*
1. Plants with leaves strictly at top of culm (bracts), or at base of culm, or absent; flowers perfect .... (3)
 3. Inflorescences not subtended by leafy bracts .... (4)
  4. Plants leafless except for bladeless basal sheaths; flowers with hypogynous bristles; achenes with thickened caps derived from style bases; culm topped with single spikelet (*Eleocharis*) .... (5)
   5. Spikelets 20 or more mm long .... (6)
    6. Stems triangular (fresh), nonseptate (examined externally when dry) .. 16. *Eleocharis mutata*
    6. Stems terete (fresh), septate (as examined externally when dry) .... 14. *Eleocharis interstincta*
   5. Spikelets < 20 mm long .... (7)
    7. Spikelets usually 8–15 mm long, fusiform or lanceolate .... 15. *Eleocharis macrostachya*
    7. Spikelets < 6 mm long, globose to ovate-lanceolate .... 13. *Eleocharis geniculata*
  4. Plants with leaf blades; flowers lacking hypogynous bristles; achenes free of style bases; culms usually bearing multiple spikelets, or single in *Abildgaardia ovata* (*Fimbristylis*/*Abildgaardia*) .... (8)
   8. Spikelet one per culm, whitish .... 1. *Abildgaardia ovata*

8. Spikelets several per culm, brown .... (9)
9. Spikelets < 4 mm long; scales with hyaline margins .... 18. *Fimbristylis cymosa* subsp. *spathacea*
9. Spikelets usually 5 mm or longer; scales with dark margins (or not translucent white) .... (10)
10. Styles 3; stems flattened and 3 mm wide ... . 17. *Fimbristylis complanata*
10. Styles 2; stems terete or if flattened < 2 mm wide .... (11)
11. Inflorescence dichotomously branched, with 2–3 orders of branching; spikelets < 3 mm wide .... 19. *Fimbristylis dichotoma*
11. Inflorescence umbellate, otherwise unbranched; spikelets > 3 mm wide (scales often pubescent) .... 20. *Fimbristylis ferruginea*
3. Inflorescences subtended by leafy bracts .... (12)
12. Leaves and bracts usually < 1 mm wide .... 27. *Torulinium filiforme*
12. Leaves and bracts mostly > 2 mm wide ...... (13)
13. Bract single, continuing axis of culm past the inflorescence (styles 2) .... 6. *Cyperus laevigatus*
13. Bracts 2 or more .... (14)
14. Bracts conspicuously whitened at base .. .. 24. *Rhynchospora nervosa*
14. Bracts green .... (15)
15. Bracts 3, subtending an apparently unbranched dense globose head (*Kyllinga*) .... (16)
16. Heads white (fresh); scales with winged keels scabrous-ciliate for most of their length; stamens 3 .... 22. *Kyllinga nemoralis*
16. Heads green (fresh); scales with unwinged keels scabrous-ciliate near the center if at all; stamens 2 ..... 21. *Kyllinga brevifolia*

15. Bracts 1–many; inflorescence not a dense globose head . . . . (17)
17. Bracts 12 or more . . . . 3. *Cyperus alternifolius*
17. Bracts 1–9 . . . . (18)
18. Plants often > 1 m tall, having leaves < 2 cm wide; spikelet-covered inflorescence axes commonly > 4 cm long (excluding spikelets); inflorescence with 3 strongly developed orders of branching (not including the spikelets); styles 2 . . . . 2. *Cyperus alopecuroides*
18. Plants < 1 m tall (infrequently taller), having leaves usually narrower than 1 cm; spikelet-covered axes usually < 3 cm long; inflorescence usually with 1 or 2 orders of branching (not including the spikelets); styles 2 or 3 . . . . (19)
19. Scales with the midvein drawn out into a cusp . . . . 4. *Cyperus compressus*
19. Scales with the midvein not protruding past the blade, or the midvein merely mucronate (20)
20. Spikelets 10 mm or more long . . . . (21)
21. Spikelets purplish . . 11. *Cyperus rotundus*
21. Spikelets greenish to straw-colored . . . . 12. *Cyperus sphacelatus*
20. Spikelets < 10 mm long . . . . (22)
22. Spikelets 8 or fewer per inflorescence ray . . . . (23)
23. Inflorescence condensed and headlike or rarely with visible rays; spikelets ascending relative to ray, 2–3 mm wide . . . . 10. *Cyperus planifolius*
23. Inflorescence uncrowded, umbellate; spikelets perpendicular to ray, 1 mm wide . . . . 28. *Torulinium odoratum*
22. Spikelets > 8 per inflorescence ray (24)
24. Scales (including those fallen from spikelets) > 30 on mature spikelets; stamen 1 . . . . 9. *Cyperus ochraceus*
24. Scales < 30; stamens 1–3 . . . . . . (25)

25. Plants viscid when fresh; bracts thick and fleshy; spikelets with dark markings, inserted digitately to form globose clusters .... 5. *Cyperus elegans*

25. Plants not viscid; bracts flat; spikelets uniformly colored, inserted pinnately to form clusters longer than broad ... . (26)

  26. Styles 2; leaves 1–2 (4) mm wide; basal portion of raylets exposed; spikelets 4–9 mm long .... 23. *Pycreus polystachyos*

  26. Styles 3; leaves > 3 mm wide; raylets absent or completely covered with spikelets; spikelets < 5 mm long .... (27)

    27. Plants 20–60 cm tall; exposed portions of rays < 1.2 cm long; spikelets straw-colored or whitish .... 8. *Cyperus luzulae*

    27. Plants up to 1–2 m tall; exposed portions of rays commonly 2–several cm long; spikelets dark brown .... 7. *Cyperus ligularis*

SPECIES DESCRIPTIONS AND SPECIMEN CITATIONS

Abildgaardia Vahl, Enum. Pl. 2: 296. 1805.

Culms tufted and filiform; *leaves* basal; *inflorescences* with usually just one (rarely 2 or 3) terminal spikelet(s); *scales* 3-nerved, deciduous, subdistichous; *stamens* 3; *style* 3-cleft and with broadened base; *achenes* verrucose. About 15 (sub)tropical species in the New World and Old World.

1. **Abildgaardia ovata** (N. L. Burm.) Kral, Sida 4 (2): 72, fig. 2. 1971. Figure 1.

Carex ovata N. L. Burm., Fl. Ind. 194. 1768.
Fimbristylis ovata (N. L. Burm.) Kern, Blumea 15: 126. 1967. FLA 3: 235.
Abildgaardia monostachya (L.) Vahl, Enum. Pl. 2: 296. 1805. Gooding et al., Fl. Barbados 73.

Small, nearly glabrous, tufted sedge to 40 cm tall; *culms* thin, under 1 mm diam.; *leaves* grasslike, stiff, narrower than 1 mm, in dense tufts, shorter than the culms; *inflorescences* lance-ovate, pale, 7–10 (20) mm long, 3–6 mm wide, often subtended by small, inconspicuous linear, hispidulous *bracts* to 6 mm long appressed to the inflorescence base, disintegrating acropetally;

spikelet generally solitary; *scales* 2-ranked, keeled, often nearly white, broadly ovate with the pronounced midrib extending as a mucro.

SPECIMENS EXAMINED. **Barbados.** ST. JOHN: In sour grass pasture near Bath Wood, 27 Mar 1937, *McIntosh & Allan 375* (BAR). ST. PETER: Speightstown, on wet marly sand, 10 Oct 1996, *Rogers 96-77* (BAR). ST. PHILIP: Mt. Pleasant, coralstone-rocky meadow on hilltop, 25 Sep 1996, *Rogers 61* (BAR, MICH); Penny Hole, sea cliffs, 27 May 1990, *Carrington & Taylor 1209* (BAR); Foul Bay, sour grass pasture, Aug 1940, *Gooding 375* (BAR). Parish unclear: Waterford, "3.8.01," "452" (BAR).

Abildgaardia ovata is a tough sedge abundant in Barbados, characteristic of exposed, sunny, often (but not necessarily) rocky sites. This species tolerates dry or wet conditions. It is abundant on the athletic field at the University of the West Indies campus, on rocky outcrops, and on wet mud in Graeme Hall Swamp. The plants are recognized by their extremely thin, densely tufted leaves, extremely thin culms, and whitish, more or less lanceolate, solitary heads with 2-ranked scales. *Abildgaardia ovata* is pantropical.

Cyperus L., Gen. Pl. 12. 1737. Sp. Pl. 44. 1753.

Culms 3-angled, usually topped by corymbose-umbellate *inflorescences* subtended by (1) several foliar *bracts; leaf blades* (usually) present at base of culm; *spikelets* not disarticulating; *flowers* perfect, lacking hypogynous bristles; *styles* 3 or rarely 2, not jointed at insertion onto ovary. Approximately 750 species, worldwide.

2. **Cyperus alopecuroides** Rottb., Descr. Pl. Rar. 20. 1772. FLA 3: 259. Figures 2, 3.

Very large glabrous, thick, slightly succulent sedge often standing over 1.5 m tall; *culm* smooth, thick, fleshy, triangular, up to 7 mm thick at the apex; *leaves* a little succulent, up to 150 cm long and 22 mm wide, smooth-margined; *inflorescence* up to ca. 40 cm tall × 60 cm wide, often with 3 well-defined orders of branching (excluding the spikelets); *bracts* ca. 4, resembling the leaves, 1.5 cm wide, up to ca. 1 m long; *rays* up to 9 (or probably more), up to 26 cm long, bare except for the apical cluster of *raylets*, these up to 11 cm long, either resembling the primary rays or covered densely with spikelets; *third-order branches* (when present) up to 4 cm long, fingerlike with a dense covering of spikelets; *spikelets* elongating to ca. 1 cm, with as many as 30 delicate lance-acuminate to oblong, apiculate *scales* ca. 1.5 mm long, having parallel greenish nerves (dry); *stamens* 2; *styles* 2; *achenes* dark brown, glossy, biconvex, elliptic to obovate.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Graeme Hall Swamp, in water at edge of woods, sunny, 22 Dec 1996, *Rogers 96-166* (BAR). ST. PHILIP: Golden Grove, drainage ditch [modified stream] through muddy pasture, in running water, clumps scattered in stream, 25 Sep 1996, *Rogers 96-64* (BAR-immature plant); same locality, 6 Dec 1996, *Rogers 96-150* (MICH); same locality, 7 Jan 1997, *Rogers 97-2* (BAR); Three Houses, around the first pond downstream from Three Houses Park, 27 Jan 1997, *Rogers 97-8* (BAR).

Prior to the present study, *Cyperus alopecuroides* had not been reported from the island. We have collected *C. alopecuroides* at three sites, all in nitrogen-rich mucky places in or immediately alongside water. The species is recognized by its massive size frequently exceeding 1.5 m tall and with leaves exceeding 2 cm wide, by its compound umbellate inflorescences frequently having three pronounced orders of branching, and by the fingerlike ultimate inflorescence axes comprised of very tightly crowded short spikelets standing out from the inflorescence axis like bristles of a bottlebrush. *Cyperus alternifolius* differs in overall appearance from *C. alopecuroides* by having well over 10 (vs. ca. 4) bracts, these of similar length and width (vs. of mixed sizes). The spikelets of *C. ligularis* are dark brown at maturity, as opposed to light brown or greenish-brown in *C. alopecuroides,* which differs further by having smooth (vs. serrulate) leaf margins. That *C. alopecuroides* has just two (vs. three) styles is unusual in *Cyperus* and distinguishes it from our other large-statured species.

Looking beyond Barbados, few West Indian sedges have the massive size of *Cyperus alopecuroides*, nor do many have inflorescences frequently showing three pronounced orders of branching and with the young spikelets crowded into thick stubby "fingers" on the raylets or on third-order branches. The pantropical *C. imbricatus* Retz. is large and has inflorescences similar to *C. alopecuroides*. The styles in *C. imbricatus*, however, are three, in contrast to the unusual condition of two in *C. alopecuroides*. Moreover, examination of *C. imbricatus* herbarium specimens at the University of Michigan Herbarium revealed a sedge less fleshy and less massive than the Barbados specimens.

Even though *C. alopecuroides* is probably indigenous to the Old World, Koyama (1979) listed it on Grenada, Guadeloupe, Marie Galante, Montserrat, Nevis, and St. Lucia, making the occurrence on Barbados almost predictable. There is a collection of it from Polk Co., Florida, too (*K. Craddock Burks 1018*, FLAS).

3. **Cyperus alternifolius** L., Mant. Pl. 28. 1767. FLA 3: 257. Gooding et al., Fl. Barbados 75. Figures 4, 5.

Highly variable sedge of wet places; *culms* often well exceeding 1 m tall, triangular, clothed at the base with bladeless sheaths; *inflorescences* up to ca. 12 cm tall and 25 cm across, often with 2 orders of branching (infrequently with small third-order branches); *rays* up to ca. 8 cm long and the *raylets* up to ca. 2–3 cm long; *bracts* ca. 12–15, uniform, abaxially scabrous, serrulate, ca. 15–30 cm long, up to 13 mm wide; *spikelets* in digitate clusters of 4–18 at apices of rays or raylets, 0.3–1 cm long, flat, lanceolate or ligulate-fusiform; *scales* ca. 2.5 mm long, tightly imbricate in chevron pattern, sharply keeled, with a pronounced midrib, lanceolate, acuminate, often apiculate; *stamens* 3; *stigmas* 3; *achenes* 3-angled.

SPECIMENS EXAMINED. **Barbados.** ST. ANDREW: Scotland District near Haggats Ministry of Agriculture Soil Conservation District facility, 21 Aug 1996, *Rogers 96-13* (BAR). ST. JOSEPH: Near Bloomsbury, swampy area within remote cow pasture, on muddy substrate, 4 Nov 1996, *McClain 96-15* (BAR). ST. MICHAEL: Codrington House, 7 Jul 1902, *Bovell 359* (BAR). Cultivated Specimen: Andromeda Botanic Gardens, 25 Feb 1997, *Rogers 97-14* (BAR).

Referred to as "umbrella sedge," this species has escaped aggressively from horticulture as an invasive pest forming massive stands in wet sites throughout much of Barbados. A second horticulturally popular sedge, encountered infrequently in Barbados but not escaped, is the enormous *Cyperus papyrus* L. *Cyperus alternifolius* is indigenous to Africa and Madagascar. It may be recognized readily in the field by its large stature and unique cluster of uniform, broad bracts reminiscent of the spokes of an umbrella. It is distinguished from the similarly large *C. alopecuroides* under that species.

4. **Cyperus compressus** L., Sp. Pl. 46. 1753. FLA 3: 251. Figures 6, 7.

Small sedge to 25 cm tall; *culm* triangular, ca. 1.5 mm diam. at the apex; *leaves* flat, grasslike, a few exceeding the culm, to ca. 27 cm × 1.5–2.2 mm wide, the sheathing bases purplish (fresh); *bracts* 3–5, up to 20 cm long × 2.2 mm wide; *inflorescence* up to 4 cm tall × 5 cm wide (excluding the bracts), simple, umbellate with *rays* to 3.3 cm long, these topped with nearly digitate clusters of 4–6 spikelets; *spikelets* (immature) 8–11 mm long, up to 3 mm wide, flattened, bearing 4–10 flowers; *scales* 3.5–4 mm long, lanceolate-ovate with hyaline margins wrapped around the flowers, and with long-attenuate, divergent tips comprised of the midrib drawn out into a short awn flanked by a pair of cusps rising from the scale margins; *flowers* with 3 *stamens* and with 3 delicate *stigmas* atop a long, threadlike style; *achene* 3-angled.

SPECIMENS EXAMINED. **Barbados.** ST. MICHAEL: Stable behind the Barbados Museum, in sunny moist overgrown lawn exposed to substantial horse waste, 28 May 1997, *Rogers 97-21* (BAR).

Not previously reported from Barbados, this small sedge turned up in a moist, grassy, high-nitrogen site unique to the island. The species distinctively has simple umbellate inflorescences with the rays bearing near-digitate clusters of spikelets. That the spikelet scales have the midveins drawn out into short awns helps with identification. *Cyperus elegans* is similar at first glance, but differs by being larger and by having thick, fleshy (vs. flat) bracts, sticky culms, and compound inflorescences. *Cyperus compressus* occurs pantropically.

5. **Cyperus elegans** L., Sp. Pl. 45. 1753. FLA 3: 257. Gooding et al., Fl. Barbados 76. Figures 8, 9.

Delicate, slender sedge; *culm* to 65 cm long, ca. 1.5 mm diam. at the apex, smooth or scabrous, viscid toward the top when fresh; sheath light brown; *leaves* linear, scabrous, numerous, equaling or longer than the culm; *bracts* 2–6 (or more), linear, viscid when fresh, resembling the leaves though sometimes thicker, to ca. 50 cm long; *inflorescence* (excluding bracts) to 16 cm tall and 16 cm wide, exhibiting 2 well-defined orders of branching excluding the spikelets (occasionally with short third-order branches); *rays* up to 12 cm long; *raylets* to 4 cm long; *spikelets* in digitate clusters of 4–16 (20) on rays and raylets, variable in length, up to 12 mm long, 3 (4) mm wide, flattened; *scales* strongly 2-

ranked, ca. 2.5–3 mm long, separating apically at maturity, giving the spikelets a roughened-serrate appearance, lance-ovate with apiculate apices and with broad margins wrapping around the black triangular *achenes; stamens* 3; *styles* 3.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Graeme Hall Swamp, 13 Apr 1989, *Carrington & Taylor 1118* (BAR); Oistins, in low area of wet mud (occasional standing water) dominated by this species, across the Coast Road from the Oistins Post Office, 5 Sep 1997, *Rogers 97-3* (BAR). ST. JOHN: Along coastal highway in a disturbed weedy field in standing water, ca. 1 km N of B.E.C. satellite dish, 23 Oct 1996, *Rogers 96-117* (BAR, MICH); same locality, 7 Nov 1996, *McClain 96-22* (BAR); stream in College Estate, Feb 1937, *McIntosh 377* (BAR); Newcastle, 5 Nov 1906, *Dash 610* (BAR). ST. PHILIP: Three Houses, around the first pond downstream from Three Houses Park, 22 Jan 1997, *Rogers 97-9* (BAR).

Cyperus elegans has spikelets similar to *C. planifolius, C. compressus*, and *C. alternifolius. Cyperus elegans* differs from these and all other Barbados sedges by being viscid when fresh, and by having uniquely long, linear, fleshy bracts. These seldom exceed 2 mm across, as encountered on herbarium specimens. *Cyperus elegans* occurs in wet (usually brackish?) sunny sites scattered in the New World tropics.

6. **Cyperus laevigatus** L., Mant. Pl. 2: 179. 1771. FLA 3: 259. Gooding et al., Fl. Barbados 76. Figure 10.

Rushlike, rhizomatous, glabrous, nearly leafless sedge; *culms* vertical and crowded, tapered, terete or flat when dry, up to 40 cm long (including the bract), 1–2 mm diam., striate (dried), bearing a single bract extending the culm axis beyond the pseudolateral inflorescence; *leaves* sheathlike; sheath brown (dried), to ca. 7 cm long, often apiculate; *inflorescences* compact, to 15 mm long × 10 mm wide, consisting of a tight cluster of up to 6 (13) sessile, flattened *spikelets*, these up to 9 mm long × 2 mm wide; *scales* imbricate, 1.2–1.6 mm long, broadly ovate, keeled, some with the keel protruding as a short point; *stamens* 3; *styles* 2; *achene* obscurely and unevenly 3-lobed.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Graeme Hall Swamp, 8 Feb 1937, *McIntosh & Allan 305* (BAR). ST. JOHN: Near stream, Martins Bay, 14 Jan 1990, *Carrington 1148* (BAR). ST. JOSEPH: Railway line at Tenby, Jul 1937, *McIntosh "435? = 305a"* (BAR).

Two searches by Rogers during January and April 1997 at

"Martin's Bay" failed to yield *Cyperus laevigatus*. The species has not turned up in a 1997 plant inventory of Graeme Hall Swamp conducted by Dr. S. Carrington of the University of the West Indies along with G. Rogers. The species is distinctively rushlike with the bract continuing the culm axis, placing the small inflorescence in a pseudolateral position. The spikelets resemble tiny rattles from rattlesnakes. The most likely Barbados sites for *C. laevigatus*, if it turns up again, are brackish stream outlets in or near St. John Parish. The species is distributed around the world in warm climates.

7. **Cyperus ligularis** L., Pl. Jamaic. Pug. 3. 1759. Gooding et al., Fl. Barbados 76. Figures 11–13.

Mariscus ligularis (L.) Urban, Symb. Antill. 2 (1): 165. 1900. FLA 3: 267.

Coarse plants in large, well-defined, pale green, glaucous, conspicuous clumps sometimes >2 m tall; *culm* sturdy, erect, 3-angled, up to 4 mm diam. at the apex.; *leaves* sometimes >1 m long, frequently a little shorter than the culm, often ca. 10 (15 basally) mm wide, sharply serrulate, the leaf bases tending to be reddish-brown; *bracts* numerous, inserted at a reddish-brown (dry) swelling, highly variable in length, the longest ca. 85 cm long, up to 8 (10) mm wide, similar to the leaves; *inflorescence* umbellate, 6–25 cm across (excluding the bracts), up to 14 cm long, with one well-defined order of branching (though often with short raylets densely covered with spikelets); *rays* up to 11 in number, up to 11 (15) cm long, the spikelets densely aggregated into dark brownish, elongate-globular, sometimes-branched heads ca. 1 cm wide (excluding branches) and up to 4.5 cm long, when branched the axes of the branches hidden by spikelets; *spikelets* 4–5 mm long, 1 mm wide, with 3–5 *scales* apparent, these ca. 2.5–2.8 mm long, ovate-lanceolate, keeled, with a midvein and with longitudinal nerves; *stamens* 3; *styles* 3; *achenes* sharply 3-angled.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Graeme Hall Swamp, 10 Feb 1937, *McIntosh & Allan 306(a)* (BAR); Coastal Road entrance to Graeme Hall Swamp, marly sand, 8 Oct 1996, *McClain 96-1* (BAR); Silver Sands Park, 8 Oct 1996, *McClain 96-2a* (BAR); area of standing water behind beach, between Silver Sands Hotel and Silver Rock Hotel, 27 Sep 1996, *Rogers 96-72* (BAR). ST. ANDREW: Dune area between beach and East Coast Rd. between Belleplaine and Barclays Park, 21 Aug 1996, *Rogers 96-19* (BAR, MICH). ST.

JOHN: Along coastal highway, low area in highly disturbed weed field, standing water, 23 Oct 1996, *Rogers 96-116* (BAR). ST. MICHAEL: Bridgetown, Careenage, on rocks, 13 Nov 1996, *Forde 96-23* (BAR). ST. PETER: Beach on coast road, under bridge, on verge of standing water, Speightstown, 10 Oct 1996, *McClain 96-5* (BAR).

Cyperus ligularis is one of the more abundant, widespread, and conspicuous sedges on Barbados. It frequently inhabits sunny, sandy, or rocky places, very commonly near the sea. It is particularly abundant and robust in localities where fresh water meets the sea, such as mouths of streams. *Cyperus ligularis* is recognized by a glaucous coloration on the stem and foliage, by its large stature (see *C. alopecuroides* for differentiation from other large sedges), by its severely saw-tooth leaf margins, and by its short, dark brown spikelets with only 3–5 scales. The spikelets are densely clustered into thick (1 cm), stubby, dark brown "fingers" on the rays and on short (hidden by spikelets) raylets. *Cyperus ligularis* grows in the New World tropics and in Africa.

8. **Cyperus luzulae** (L.) Rottb. ex Retz., Obs. Bot. 4: 11. 1786. FLA 3: 253. Figures 14, 15.

Plants up to 20–60 cm tall; *culms* 3-angled, to 2 mm diam. at the apex, smooth; *leaves* sometimes longer than the culm, up to 5 mm wide; *bracts* usually 6–9, up to ca. 35 (occasionally more) cm long, to 5 (6) mm wide, marginally scabrous; *inflorescence* compact-umbellate, to 7 cm wide and 4 cm tall, with 1 pronounced order of branching (second-order branches, when present, hidden beneath spikelets); *rays* usually with the lower portions bare, to 3 cm long; *spikelets* in dense, conical to cylindric, hoary-white heads at the tips of the rays, the heads variable in size, up to 1.5 cm × 1.5 cm, often with cryptic second-order branching within the head; *spikelets* flattened, up to 5 mm long × 2 mm broad; *scales* distichous, 1.4–1.6 mm long, strongly keeled, lanceolate (or infrequently oblong); *stamen* 1; *styles* 3; *achene* 3-angled.

SPECIMENS EXAMINED. **Barbados.** ST. ANDREW: Turner's Hall Woods, damp pasture in woods, Nov 1940, *Gooding 602* (BAR); same locality, 17 Dec 1996, *Rogers 96-159* (BAR). ST. JOSEPH: Near Bloomsbury, pasture in dairy farm, along road between Sturges and Castle Grant, 4 Nov 1996, *McClain 96-11* (BAR, MICH); same locality, 11 Sep 1996, *Rogers 96-50* (BAR); same locality, 20 Sep 1996, *Rogers 96-68* (BAR). ST. THOMAS: Bloomsbury, swampy ground, 15 Feb 1990, *Carrington & Taylor 1174* (BAR). ["Bloomsbury" collections are recorded in two different parishes because the Bloomsbury area lies at the border between St. Joseph and St. Thomas.]

At a glance this handsome species suggests a small version of *Cyperus ligularis*, and is readily recognized in the field by the distinctive hoary-white (vs. dark brownish) coloration of its more congested, shorter spikelet clusters. Unlike *C. ligularis*, the leaves (but not the bracts) of *C. luzulae* are smooth-margined. The species is widespread in the New World tropics.

For a discussion of nomenclatural complications with the combination "*Cyperus luzulae*," see McVaugh (1993), who justifiably suggested a citation for this combination altered from that usually cited. We have followed McVaugh's suggestion.

9. **Cyperus ochraceus** Vahl, Enum. Pl. 2: 325. 1805. FLA 3: 254. Figure 16.

Large sedge 30–70 cm (or sometimes more) tall; *culm* triangular, smooth, to ca. 5 mm diam.; *leaves* to ca. 80 cm long × 2–8 mm wide, scabrous-margined, long-tapered to a narrow tip; *inflorescence* to 10 cm wide × 8 cm tall (excluding the bracts); *bracts* several, of uneven lengths, resembling the leaves, to 62 cm long; *orders of branching* 2 (and with the long mature spikelet axes adding a third order of branching); *rays* to 7 cm long, the *raylets* to 2 cm long; *spikelets* numerous in loose umbellate clusters, to 15 (20) mm long, flattened, bearing many small, tightly imbricated scales, these falling from the bases of the rachillae and giving them the appearance of third-order branches; *scales* inserted at angles of over 45 degrees, beak-shaped, brown when dry, 1.5–1.8 mm long, the keel flattened (resembling a flat-bottomed boat); *stamen* 1; *styles* 3; *achenes* triangular.

SPECIMENS EXAMINED. **Barbados.** ST. PETER: Speightstown, dry drainage ditch just S of Almond Beach Resort, 12 Mar 1998, *Rogers 98-18* (BAR).

This distinctive slender sedge ranges in height to sometimes ca. 1 m, with leaves and bracts narrow. The mature compound-umbellate inflorescence has long rays, well-developed and exposed raylets, and long mature spikelets. This species and *Cyperus luzulae* are the only two Barbados species of *Cyperus* having just one stamen per flower.

Cyperus ochraceus has not been previously reported for Barbados. It was brought to our attention by University of the West

Indies student Karen Greenidge, who collected it near her home in Speightstown during the winter of 1996–97. The original site has been destroyed by construction activity. The Rogers collection comes from a second site, likewise discovered by Greenidge near the lost site.

Cyperus ochraceus resembles *C. surinamensis* Rottb., which likewise has one stamen per flower, but which is not known from Barbados. The Barbados sedge is referred to *C. ochraceus* because our material has smooth culms (vs. scabrous in *C. surinamensis*), spikelets comparatively blunt at the tips (vs. acute in *C. surinamensis*), and scales generally inserted at angles greater than 45 degrees (vs. strongly ascending scales in *C. surinamensis*). Moreover, *C. surinamensis* appears to tend toward scales shorter than 1.5 mm (see Strong 1996) as opposed to scales generally exceeding this length on the Barbados sedge. *Cyperus ochraceus* is widespread in tropical and subtropical regions from the U.S. to Argentina.

10. **Cyperus planifolius** L. C. Rich., Acta Soc. Hist. Nat. Paris 1: 106. 1792. Gooding et al., Fl. Barbados 77.
Figures 17, 18.

Mariscus planifolius (L. C. Rich.) Urban, Symb. Antill. 2 (1): 165. 1900. FLA 3: 268.

Cyperus brunneus sensu Griseb., Fl. Brit. W. Ind. 565. 1864, non Sw. 1797 (see discussion).

Coarse, stiff, robust, rhizomatous, often pale green, glabrous (except for scabrous foliar margins) sedge; *leaf sheaths* dark-colored, often purplish (dried); *culms* sharply triangular, to 60 cm tall, 1.5–2 (3) mm diam. apically; *leaves* to 55 cm long (sometimes exceeding the culm) and up to 5–6 mm wide, serrulate to nearly smooth along the margins; *inflorescence* dense, compact-umbellate, up to 9 cm wide and 5 cm tall, usually more or less spherical and with the rays difficult to discern, these 5–6 in number, to 5 cm long, sometimes devoid of spikelets toward the base; *bracts* resembling the leaves, 4–5, of unequal lengths (with one bract tending to be far longer than the others), up to 30 (40) cm long and 4 (7) mm wide; *spikelets* to 15 (18) mm long, up to 3 mm wide, with up to 10–14 (16) distichous scales 3–3.5 mm long, these broadest above the middle, exhibiting strongly developed longitudinal nerves, often purplish (dried), having green (or brown) keeled midribs tending to protrude past the scale apex; *stamens* 3; *styles* 3; *achenes* 3-angled, obovate.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Entrance to Graeme Hall Swamp, south coastal road, marly sand, 8 Oct 1996, *McClain 96-2b* (BAR), *96-3a* (BAR), *96-3b* (BAR); on backside of seaside dunes, between Silver Sands Hotel and Silver Rock Hotel [in Silver Sands Park], 27 Sep 1996, *Rogers 96-73* (BAR, MICH). ST. MICHAEL: Bridgetown, swampy land, railway lands, Oct 1940, *Gooding 600* (BAR). ST. PHILIP: Penny Hole, sea cliff, 27 Mar 1990, *Carrington & Taylor 1210* (BAR). No locality data: 7 Jul 1902, *Bovell 274* (BAR). No locality data and no collector data: Oct 1869, Herbarium, Royal Botanic Gardens, Trinidad and Tobago *3162* (BAR).

Authors are divided on the question of whether *Cyperus brunneus* Sw., Fl. Ind. Occ. 1: 116, 1797 is best interpreted as a synonym of *C. planifolius* (1792). For example, Koyama (1979) treated the two as distinct in contrast with Correll and Correll (1982) who placed them in synonymy. We find Barbados specimens matching Koyama's description of *C. brunneus* to intergrade with those matching descriptions of *C. planifolius* and tentatively suspect, from our narrow standpoint, synonymy to be the better choice. A proper investigation of the matter requires examination of the types and materials from throughout the ranges of the two entities.

Habitats for *Cyperus planifolius* are diverse, though often sandy. In Barbados it is most abundant on sand dunes behind beaches. This species is found primarily around the Caribbean.

11. **Cyperus rotundus** L., Sp. Pl. 45. 1753. FLA 3: 250. Gooding et al., Fl. Barbados 78. Figures 19, 20.

Slender, wandlike, glabrous (except for minutely serrulate foliar margins), stoloniferous, weedy, highly variable sedge with the rhizome often bearing a tuber; *culm* 18–60 cm tall, 1.5 mm diam. apically, slender, triangular, smooth; *leaves* sometimes numerous and forming "rosettes" of up to ca. 15, having a light brown sheathing base, shorter than the culm, 6–26 cm long × 2–5 mm wide, the lateral nerves strongly developed on the broader leaves; *bracts* often 2 or 3, leafy, modest, one bract generally longer than the other(s), up to 18 cm long, though usually much shorter; *inflorescence* up to 10 cm long and 9 cm wide, with 1 or 2 orders of branching (excluding the spikelets), umbellate, loose, with 2–5 unequal rays up to 8 cm long; *raylets* to 2 cm long; *spikelets* uncrowded, 2–many per ray or raylet, sleek, narrow, fingerlike, 0.5–3 cm long, 1–1.5 mm wide, dark purplish-brown (fresh and dry); *scales* 3–3.2 mm long, tightly appressed, ovate, dark purplish-brown, with greenish keel; *stamens* 3; *styles* 3; *achenes* 3-angled.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Entrance to Graeme Hall Swamp, south coastal road, marly sand, 8 Oct 1996, *McClain 96-4* (BAR); Oistins, in low area of wet mud (occasional standing water) dominated by *Cyperus elegans*, across road from Post Office, 5 Sep 1997, *Rogers 97-38* (BAR). ST. GEORGE: Roadside ditch, dominant plant between road and canefield along road connecting highways 4 and 5 via Carmichael, 15 Nov 1996, *Rogers 96-132* (BAR, MICH). ST. JOSEPH: Andrews Plantation, Oct 1935, *Mayers 2* (BAR). ST. MICHAEL: Univ. of the West Indies campus in full sun on disturbed ground, 20 Aug 1996, *Rogers 96-9* (BAR, MICH). ST. PETER: Speightstown, beach along the coast road on marly sand, 10 Oct 1996, *McClain 96-6* (BAR). ST. PHILIP: Three Houses, the first pond downstream from Three Houses Park [in cultivated field adjacent to pond], 27 Jan 1997, *Rogers 97-10* (BAR).

A highly variable, adaptable, pervasive agricultural/horticultural pest known as "nutgrass," appearing throughout Barbados on dry or wet disturbed sites. The species is recognized by its few, very long, purplish spikelets (cf. the apparently rare *Cyperus sphacelatus*). *Cyperus rotundus* is found worldwide.

12. **Cyperus sphacelatus** Rottb., Descr. Pl. Rar. 21. 1772. FLA 3: 250. Gooding et al., Fl. Barbados 78. Figure 21.

Slender wandlike, glabrous (except for foliar margins) sedge; *culm* slender, bare, up to 20 cm long, topped by an umbellate inflorescence and long, leaflike bracts; *leaves* grasslike, up to 25 cm long and 2 mm wide, most shorter than the culm; *bracts* ca. 3, of unequal lengths, the largest to 20 cm long and 2 mm wide; *rays* 4–6, up to ca. 5 cm long, free of spikelets toward the base; *spikelets* 5–12 per ray, up to 12 mm long and slightly exceeding 1 mm wide, fingerlike, narrow, sleek, light khaki (infused with patches of darker coloration visible under magnification) when dry; *scales* lanceolate, ca. 2.5 mm long, with a thick keel darker than the surrounding tissues; *stamens* 3; *styles* 3; *achenes* dark brown, smooth, 3-angled.

Cyperus sphacelatus is known from Barbados from just one specimen: ST. PHILIP: Three Houses, bank of stream, Aug 1940, *Gooding 649* (BAR; annotated as *C. sphacelatus* by R. A. Howard, 1990). Our description comes entirely from this specimen, which resembles *C. rotundus*. The former differs from *C. rotundus* by having scales of lighter overall color (predominantly light-khaki vs. predominantly purplish-brown), a reportedly less pronounced wing on the rachilla (our limited material shows *C. sphacelatus* to have a substantial wing), a reportedly annual habit, and the absence of a rhizome. Gooding et al. (1965) further distinguished *C. sphacelatus* by a tendency toward moist habitats as opposed to *C. rotundus* being a weed of cultivated ground. We find this distinction weak, since the many habitats occupied by *C. rotundus* include moist places.

We have failed to encounter *Cyperus sphacelatus* despite multiple searches of the 1940 collection locality and surrounding area. The entire area is occupied by a park, agricultural land, a highly disturbed stream, small gully, and small human-made ponds. Substantial alteration since 1940 is certain. *Cyperus rotundus* is presently abundant in the area. *Cyperus sphacelatus* occurs in the New World tropics and in Africa.

Eleocharis R. Br., Prodr. Fl. Nov. Holl. 224. 1810.

Spikelets solitary, terminating the culm; *flowers* with hypogynous bristles; *stamens* 3; *style* jointed at thick, persistent *style base*. Approximately 120 species distributed worldwide.

13. **Eleocharis geniculata** (L.) Roem. & Schult., Syst. Veg 2: 150. 1817. FLA 3: 232. Gooding et al., Fl. Barbados 79. Figure 22.

Scirpus geniculatus L., Sp. Pl. 48. 1753.
Eleocharis caribaea (Rottb.) Blake, Rhodora 20: 24. 1918.

Variably sized, clump- or mat-forming sedge; *culms* wiry, threadlike, up to 1 mm diam. and 30 cm long (though often far shorter); *leaves* represented only by short, inconspicuous sheaths at the base of the culm; *spikelets* cone-shaped, to 6 mm long × 3 mm wide, much wider than the culm; *scales* 1.6–2 mm long, elliptic to obovate, acute to rounded apically, with a pronounced green midrib; *styles* 2; *achenes* dark brown and shiny, with a conspicuous apical tubercle; *hypogynous bristles* much exceeding the achene.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Graeme Hall Swamp, full sun, mud on side of water-filled ditch, 11 Jun 1997, *Rogers 97-23* (BAR); Graeme Hall Swamp, 8 Feb 1937, *McIntosh & Allan 303* (BAR). ST. ANDREW: Sedge Pond, marly soil near edge of pond, Feb 1941, *Gooding 303* (BAR);

near Haggats, wet soil on bank where road leading E from Chalky Mt. to Highway 2 crosses stream, sunny, 21 Aug 1996, *Rogers 96-14* (BAR, MICH). ST. JOSEPH: Bathsheba, damp places, grass land near sea, 7 Jan 1918, [collector unclear] *8678* (BAR). ST. THOMAS: Bloomsbury, swampy ground, 15 Mar 1990, *Carrington & Taylor 1173* (BAR).

Eleocharis geniculata, though highly variable in size, is by far the smallest-statured of the *Eleocharis* species on Barbados. Its solitary terminal spikelets are under 6 mm long. The plants occur on swampy ground and along streams in shade or sun, forming thick clumps or sometimes mats. The species is pantropical.

14. **Eleocharis interstincta** (Vahl) Roem. & Schult., Syst. Veg. 2: 149. 1817. FLA 3: 226. Gooding et al., Fl. Barbados 79. Figures 23, 24.

Scirpus interstinctus Vahl, Enum. Pl. 2: 251. 1805.

Plants robust, rhizomatous, sometimes forming dense monospecific stands; *culms* clumped, terete, septate (septa visible externally when dry), to 1 m tall, to 6 mm diam. (dry and pressed); *leaf sheaths* clasping the culm tightly, often purplish (dry), bladeless, to 22 cm long; *spikelet* single, to 40 mm long × 7 mm wide (before bracts spread), terminating the culm, with anthers and styles exposed far before the culm attains full length; *scales* 4–5 mm long, spirally arranged, oblong, obtuse apically with a colorless-translucent wavy apical margin; *style* with 3 short branches; *achene* obovate, flat, bearing several retrorsely barbed hypogynous bristles.

SPECIMENS EXAMINED. **Barbados.** ST. JOHN: Bath, stream near Bayview, May 1946, *Gooding 408* (BAR). ST. JOSEPH: Cadbury, pond at margin, 18 Jul 1937, *McIntosh 408* (BAR); pasture in dairy farm near Bloomsbury, along road between Sturges and Castle Grant, low wet area, 11 Sep 1996, *Rogers 96-49* (BAR, MICH). Parish unknown: Henson's Lily Pond, Jan 1937, *Allan 408a* (BAR).

Eleocharis interstincta resembles *E. mutata* in having a large size, a tendency to form monospecific lawns in wet sites, and tall, leafless culms topped with long cylindric spikelets that reveal anthers and styles while the culm is still short. *Eleocharis interstincta* has terete septate culms, whereas *E. mutata* has triangular (fresh) nonseptate culms. *Eleocharis interstincta* ranges from the U.S. to Brazil.

15. **Eleocharis macrostachya** Britton in Small, Fl. Southeast.

U.S. 184. 1903. FLA 3: 230. Gooding et al., Fl. Barbados 80. Figure 25.

Slender, densely tufted sedge to a little over 50 cm tall; *culm* 1–1.5 mm diam.; bases of culms enclosed by reduced bladeless sheaths; *spikelets* 8–15 mm long × 3–5 mm wide, with ligulate to lanceolate *scales* acute or acuminate apically, ca. 3.2 mm long, the midrib narrow and failing to reach the apex; *styles* 2.

Eleocharis macrostachya has been collected only once in Barbados, in fact only once in the Lesser Antilles (Koyama 1979). The sole Barbados specimen, from St. Joseph Parish, is labeled "Herbarium, Department of Agriculture, Barbados, Aug 1904, No. *545*" (BAR). The identity of this odd collection has been confirmed on two occasions prior to the present study. According to Koyama (1979), *E. macrostachya* ranges from Canada to Argentina.

16. **Eleocharis mutata** (L.) Roem. & Schult., Syst. Veg. 2: 155. 1817. FLA 3: 226. Gooding et al., Fl. Barbados 80. Figures 26, 27.

Scirpus mutatus L., Pl. Jamaic. Pug. 6. 1759.

Tall, robust rhizomatous sedge tending to form extensive monospecific stands; *culms* to 75 cm tall, 3–7 mm wide (dried and pressed), tapered, sharply triangular; *leaves* represented only by sheaths up to 28 cm long; *spikelets* cylindric, solitary on the culm tip, to 4.5 cm long, 5–8 mm wide; *scales* ca. 4 mm long, broadly oblong, rounded and sometimes erose at the tip, the margins broad and hyaline, midrib very broad; *styles* 3 (2); *achenes* 1.5 mm long, 1 mm wide, with pronounced longitudinal striations, and with more subtle, epidermal horizontal striations; *style base* dark-colored, deltoid; *hypogynous bristles* about as long as or a little longer than the achene, with retrorse cilia.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Graeme Hall Swamp, dominant understory herb, forming a lawn throughout much of the swamp, 9 Nov 1996, *Rogers 96-128* (BAR, MICH); Graeme Hall Swamp, 8 Feb 1937, *McIntosh & Allan 302* (BAR); Graeme Hall Swamp, 13 Apr 1989, *Carrington & Taylor 1117* (BAR); Chancery Lane Swamp, in the marsh, standing water, abundant, 23 Nov 1996, *Rogers 96-138* (BAR). ST. PHILIP: Three Houses, the first pond downstream on the Three Houses River from the park, 27 Jan 1997, *Rogers 97-11* (BAR).

Eleocharis mutata is a large species with uniquely (for *Eleo-*

charis on Barbados) triangular culms. It is capable of forming immense monospecific "lawns" in wet sites, as it does in Graeme Hall Swamp, where this is the dominant herbaceous species. *Eleocharis mutata* occurs in the New World tropics and in Africa.

Fimbristylis Vahl, Enum. Pl. 2: 285. 1805, *nom. cons.*

Tufted sedges with thin *culms* much taller than the strictly basal leaves. *Bracts* present but generally less well developed than in *Cyperus*. *Inflorescences* umbellate or thyrsiform, with fusiform to globose *spikelets*. *Flowers* perfect, lacking hypogynous bristles; *stamens* and *styles* 2 or 3, the styles deciduous and often flattened and fimbriate. Approximately 150 species, mostly of the Old World.

17. **Fimbristylis complanata** (Retz.) Link, Hort. Berol. 1: 292. 1827. FLA 3: 236. Figure 28.

Scirpus complanatus Retz., Observ. Bot. 5: 14. 1789.

Robust sedge to ca. 80 (100) cm tall; *culm* flat, 3 mm wide; *leaves* up to 58 cm long × 5 mm wide, scabrous marginally; *inflorescence* to 9 cm tall × 11 cm wide, complex, open, thyrsiform, with up to 3 orders of branching (excluding spikelet axes), subtended by 1 or more foliar *bracts* up to 11 cm long × 4 mm wide, these as wide as or wider than the culm; *spikelets* fusiform, 3.5–5 mm long, usually ca. 1 mm wide; *scales* ca. 2.5 mm long, lanceolate, keeled, with a thick midrib extending into a short mucro, the margins thin; *stamens* and *styles* 3, the stigmas much shorter than the flattened style; *achene* elliptic-obovate, roughened on the surface.

SPECIMENS EXAMINED. **Barbados.** ST. ANDREW: Highway 2 between Baxters and Haggats, roadside ditch, 11 Sep 1996, *Rogers 96-44* (BAR); Highway 2, 1.6 km S of road to Chalky Mt., roadside weed, 18 Sep 1996, *Rogers 96-54* (BAR, MICH).

This sedge was previously unreported in Barbados. It is easily recognized by its broad, flat culm topped with a particularly complex thyrsiform inflorescence. The spikelets are distinctively narrow. The Barbados localities are open, disturbed, and sunny. *Fimbristylis complanata* is pantropical.

18. **Fimbristylis cymosa** R. Br., Prodr. Fl. Nov. Holl. 228. 1810, subsp. **spathacea** (Roth) T. Koyama, Micronesica 1: 83.

1964. FLA 3: 238. Gooding et al., Fl. Barbados 81 (as "*F. cymosa*"). Figure 29.

Fimbristylis spathacea Roth, Nov. Pl. Sp. 24. 1821.

Wiry, tough, tufted sedge; *culm* to 60 (100) cm tall, often rising from a trunklike, thick, congested, vertical base; *leaves* highly variable, numerous and crowded, shorter than the culm, up to 36 cm long (though often much shorter) × 2 mm wide (sometimes wider at the base), frequently thickened, the apices often rounded; *inflorescence* compact with numerous spikelets, up to 4.5 cm broad × 2.8 cm tall; *bracts* 1 (or few), up to 3 cm long × 3 mm wide, lanceolate; *orders of branching* (excluding the spikelets) 2–3, with the axes tending to curve; *spikelets* light to dark brown, (2.5) 3–4 mm long, 2 mm wide; *scales* 1.3–2 mm long, lance-ovate with hyaline margins and usually rounded to acute apices; *stamens* 2; *styles* 2.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Between Silver Sands Hotel and Silver Rock Hotel, sandy substrate behind the beach, 27 Sep 1996, *Rogers 96-71* (BAR, MICH); Graeme Hall Swamp, 13 Apr 1989[?], *Carrington & Taylor 1113* (BAR) [Note—an apparent duplicate specimen with the same collection number is dated "13 Apr 1990." Other collections in the Carrington & Taylor collection series indicate the 1989 date as more likely to be correct.]; Maxwell Coast, near swampy land west of "Calais," May 1940, *Gooding 434* (BAR). ST. ANDREW: Along coastal highway between Belleplaine and Barclays Park, on sandy dunes above beach, 4 Sep 1996, *Rogers 96-32* (BAR); stream bank near bridge on road leading to Highway 2 coming E from Chalky Mt. [There are two roads leading from Chalky Mt. onto Highway 2. This is the more southern, intersecting Highway 2 near Haggats.], 21 Aug 1996, *Rogers 96-17* (BAR). ST. JOSEPH: Railway line at Tenby, Jul 1937, *McIntosh 434* (BAR). ST. PHILIP: Ragged Point Lighthouse, rocks overlooking the sea, 25 Sep 1996, *Rogers 96-65* (BAR).

Authorities disagree on the appropriateness of treating the widespread two-styled "*Fimbristylis spathacea*" as distinct from the Old World, three-styled *F. cymosa*. Koyama (1979) and McVaugh (1993) both discuss this, and supply references to further discussion. Adams (1992) noted that some New World material has three styles. Evidence for treatment as separate species is not compelling, and consequently we follow Koyama. *Fimbristylis cymosa* subsp. *spathacea* is pantropical.

19. **Fimbristylis dichotoma** (L.) Vahl, Enum. Pl. 2: 287. 1805. FLA 3: 242. Gooding et al., Fl. Barbados 81. Figure 30.

Scirpus dichotomus L., Sp. Pl. 50. 1753.

Plants to 70 (80) cm tall (sometimes very reduced); *culms* much exceeding the leaves, slender (up to ca. 1 mm diam.); *leaves* 0.75–1.5 (2) mm wide, to 42 cm long, rounded or acute apically, serrulate marginally; *inflorescence* sometimes with one or more leafy bracts (0.5) 1–7 cm long × 1–1.5 mm wide, the inflorescence up to 10 cm long × 9 cm wide, loose and open, with 2 or 3 orders of dichotomous branching (including spikelet axes), having wirelike *rays* up to 4.5 cm long and *raylets* up to 1.5 cm long; *spikelets* (3) 5–11 mm long, 3 mm wide; *scales* 2–2.2 mm long, broadly ovate, with thick conspicuous midrib (continuing as stubby mucro) and thin margins; *achene* lenticular with longitudinal markings, bearing 2 *styles*; *stamen* 1 (or reportedly 2).

SPECIMENS EXAMINED. **Barbados.** ST. JOSEPH: Maynards, pasture, Oct 1935, *Mayers 1* (BAR); Bathsheba, grassland by sea, "7.1.18," [collector unclear] *8677* (BAR); near Bloomsbury, pasture in dairy farm along road between Sturges and Castle Grant, low wet area, 11 Sep 1996, *Rogers 96-51* (BAR, MICH).

Fimbristylis dichotoma has dichotomously branched inflorescences with 2–3 orders of branching. The culms are far narrower (ca. 1 mm vs. 3 mm diam.) than in the similar *F. complanata*. *Fimbristylis dichotoma* is almost worldwide in tropical and temperate regions.

20. **Fimbristylis ferruginea** (L.) Vahl, Enum. Pl. 2: 291. 1805. FLA 3: 241. Gooding et al., Fl. Barbados 81. Figures 31, 32.

Scirpus ferrugineus L., Sp. Pl. 50. 1753.

Robust, variable, rushlike sedge with tall (to ca. 1 m), terete, tapered *culms* in tufts; *leaves* inconspicuous, much shorter than the culm, to 26 cm tall, under 2 mm wide, smooth to slightly scabrid on the margins, often represented only by sheaths; *bracts* inconspicuous, linear, hispidulous marginally, to 3.5 cm long × up to 2 mm wide (at the base); *inflorescences* up to 4 cm tall and 3 cm broad; *spikes* umbellate with the *rays* unbranched and of uneven lengths; *spikelets* 2–numerous, light brown (fresh and dry), (5) 7–9 (10) mm long (excluding portions of rachilla from which scales have fallen), 3–5 (7) mm wide; *scales* 3.7–4 mm long, broadly elliptic, shallowly (or not) keeled, with minute pubescence on the keel (or variably spreading across the abaxial face of the scales), mucronate; *stamens* 3; *styles* 2.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Graeme Hall Swamp, in and near standing water, much along stream bank, 9 Nov 1996, *Rogers 96-129* (BAR, MICH); Graeme Hall Swamp, Feb 1937, *McIntosh 304a* (BAR); Dover Woods, side of brackish swamp on sandy soil, May 1940, *Gooding 304* (BAR). ST. JOHN: Bath, stream near Bayview, May 1940, *Gooding 304* (BAR) [note repeated "species" number for two different Gooding collections]. ST. LUCY: Seashore, along inlet at River Bay, 19 Dec 1996, *Rogers 96-165* (BAR).

Fimbristylis ferruginea is a tall robust *Fimbristylis* with large (over 3 mm diam.) uniquely rust-colored spikelets. This species is pantropical.

Kyllinga Rottb., Descr. Icon. Rar. Pl. 12. 1773, *nom. cons.*

Bracts consistently 3 (in ours): one vertical and the others flanking it; *inflorescences* tightly congested into a burr; *spikelets* 1-flowered, with empty basal scales, disarticulating at the base, bases of scales confluent onto the rachilla; *styles* 2; *achenes* lenticular and 2-sided. Approximately 140 species distributed throughout much of the world.

21. **Kyllinga brevifolia** Rottb., Descr. Icon. Rar. Pl. 13. 1773. FLA 3: 283. Figure 33.

Cyperus brevifolius (Rottb.) Endl. ex Hassk., Cat. Hort. Bogor. 24. 1844. Gooding et al., Fl. Barbados 75.

Modest grasslike, rhizomatous sedge; *culms* 10–33 cm tall, soft, slender, few-leaved at base; *leaves* narrowly linear, shorter than or occasionally as long as the culm, 1–3 mm wide, scabrid; *basal sheathing leaf bases* membranous, purplish-brown (fresh); *bracts* 3, about as wide as the leaves, with one upright and up to 9 cm long, flanked by two additional, divergent, subequal bracts to 5.5 cm long; *inflorescences* comprising a single greenish (fresh) to straw-colored, burrlike, globose to slightly elongate head up to 7 mm long × 7 mm wide; *spikelets* compressed, 2–3 mm long, single-flowered, with one empty scale (the fertile scale and empty scale meeting face-to-face, unequal, and often with divergent apices, giving the spikelet a horned appearance); *scales* ovate-lanceolate, as long as the spikelet, multinerved with a prominent midrib extending into a mucro, the midrib usually scabrous-ciliate near its middle; *stamens* 2; *styles* 2; *achene* lens-shaped.

SPECIMENS EXAMINED. **Barbados.** ST. JOSEPH: Pasture, growing on muddy substrate near Bloomsbury, 11 Sep 1996, *Rogers 96-52* (BAR). ST. THOMAS: Swampy ground, Bloomsbury, 15 Feb 1990, *Carrington & Taylor 1176* (BAR); Walkes Spring Gully, 21 Oct 1937, *McIntosh & Allan 448* (BAR).

Kyllinga nemoralis is similar but has white (vs. green) heads, scales with winged keels scabrous-ciliate along most of the length of the keel (vs. scabrous-ciliate at the center of the keel, if at all), and 3 (vs. 2) stamens. *Kyllinga brevifolia* is subtropical and tropical worldwide.

22. **Kyllinga nemoralis** (J. R. & G. Forst.) Dandy ex Hutch., Fl. W. Trop. Africa, ed. 1, 2, 2: 487. 1936. Figure 34.

Thryocephalon nemorale J. R. & G. Forst., Char. Gen., Pl. 130. 1776.

Grassy, weedy, strongly rhizomatous, glabrous sedge rising to about 40 cm tall; *culms* sharply 3-angular, to about 1.2 mm diam. at the apex; *basal sheathing leaf bases* purplish (fresh); *leaves* not entirely basal, the blades shorter than the culms, to 14 cm long × 4 mm wide, V-shaped in transverse section; *bracts* 3 or 4, reflexed, unequal in length, similar to the leaves in width (or narrower) and overall appearance but shorter, to 11 cm long; *flowering head* single, sessile, white (fresh and nearly white when dried), globose or a little longer than broad, tightly congested, to ca. 6 (7) mm long; *spikelets* generally 1-flowered, the *scales* nearly equal and defining the length of the spikelets, to ca. 3 mm long, strongly flattened into an envelope with a winged keel, the wing with a scabrous-ciliate margin for most of its length; *stamens* 3; *styles* 2, about as long as the flattened, dark-colored achene.

SPECIMENS EXAMINED. **Barbados.** ST. JOSEPH: Weed on grounds of Andromeda Botanic Gardens, 8 Dec 1997, *Rogers 97-58* (BAR); same locality, *13 Oct 1989, Carrington 1090* (BAR).

Kyllinga nemoralis may be confused with *K. brevifolia*. For a recent treatment of *K. nemoralis* in Trinidad see Adams (1992). In Barbados, *K. nemoralis* is known only as a lawn weed. The abundant weedy population in a minimally tended lawn area at Andromeda Botanic Gardens may owe its arrival to plants, seeds, and soils imported during the post-1954 development of the facility. As reported by Dr. C. Dennis Adams (pers. comm.), the pantropical species will probably turn up increasingly in the West Indies. By 1992 he had recorded it from Jamaica, St. Kitts, Dominica, and Trinidad and Tobago.

Pycreus P. Beauv., Fl. d'Oware 2: 48, t. 86. 1807.

Spikelets flattened, with distichous scales; *flowers* without hypogynous bristles; *ovaries* 2-carpellate; *achenes* flattened and two-sided; *styles* 2. Not strongly distinguished from *Cyperus*. Approximately 70 species throughout much of the world, mostly in Africa.

23. **Pycreus polystachyos** (Rottb.) P. Beauv., Fl. d'Oware 2: 48. 1807. FLA 3: 261. Figure 35.

Cyperus polystachyos Rottb., Descr. Pl. Rar. 21. 1772. Gooding et al., Fl. Barbados 77.

Slender sedge to 40–70 cm tall; *culms* up to ca. 2 mm diam. near the apex; *leaves* up to 43 cm long × 1–2 (4) mm wide; *bracts* 3–6 in number, very unequal, 14–40 (45) cm long, to 5 mm wide, the shorter ones stiff and perky, drooping when long, resembling the leaves though sometimes broader, often yellowish (fresh); *inflorescence* umbellate, up to 6 cm tall × 10 cm wide; *rays* 5–8 in number, up to 6 cm long, free of spikelets toward the base; *raylets* very short and generally hidden by spikelets, sometimes with short 3rd- or 4th-order branches (excluding the rachillae); *spikelets* flattened with imbricate scales in a chevron pattern, up to 8–10 mm long × 1–1.5 mm wide, straw-colored when dry, narrowly lanceolate; *scales* 6–18 per spikelet, 1.5–1.9 mm long, lanceolate, often (dry) with green; *stamens* 1 or 2.

SPECIMENS EXAMINED. **Barbados.** CHRIST CHURCH: Graeme Hall, Apr 1989, *Carrington & Taylor 1114* (BAR). ST. JOHN: Low area in disturbed field, standing water, about 1 km N of B. E. C. satellite dish, 23 Oct 1996, *Rogers 96-118* (BAR, MICH); same locality, 4 Nov 1996, *McClain 96-20* (BAR). ST. JOSEPH: Maynard's, Aug 1936, *Mayers 376* (BAR). ST. PHILIP: Marsh in stream near Palmer's, 4 Apr 1937, *McIntosh 376a* (BAR).

Pycreus polystachyos is a medium-sized sedge of wet, muddy, sunny places. Its distinctive features include a tendency toward yellow-green coloration (at least in Barbados), inflorescences with straw-colored lanceolate spikelets in loose short-branched clusters borne by elongate rays, and two styles. Some contemporary authors place this species in *Cyperus*. *Pycreus polystachyos* occurs worldwide in warm-temperate, subtropical, and tropical regions, as far north as Japan. It is abundant in Graeme Hall Swamp.

Rhynchospora Vahl, Enum. Pl. 2: 229. 1805, *nom. cons.*

Dichromena Michx., Fl. Bor.-Amer. 1: 37. 1803.

Distal *flowers* in spikelet staminate; *bracts* (in ours) whitened adaxially at the base; *styles* 2 (1); *achenes* lens-shaped, topped with a persistent *style base*. Approximately 250 species, cosmopolitan.

24. **Rhynchospora nervosa** (Vahl) Boeck., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn III. 1: 143. 1869. FLA 3: 306. Gooding et al., Fl. Barbados 82. Figure 36.

Dichromena nervosa Vahl, Enum. Pl. 2: 241. 1805.

Tough glabrous to heavily white-ciliate sedges of highly variable stature and form, to 30 (50) cm tall; *culms* 3-angled, 1–1.5 mm diam. near the apex; *leaves* (rarely) up to 35 cm long × 5 mm wide, shorter than or longer than the culm, featuring a strongly developed midrib; *bracts* generally ca. 6 in number, 8–14 cm long, up to 3 (4) mm wide, tapered, with bright white (fresh and dry) basal-adaxial markings; *inflorescences* headlike, globose or nearly so, up to 1.5 cm tall × 2 cm broad (excluding the bracts) with numerous, crowded, sessile whitened *spikelets* 5–8 mm long × 2–3 mm wide; *scales* 4.5–5 mm long, lanceolate, with a narrow keel corresponding to the midrib; *stamens* 3; *styles* 2; *achenes* lens-shaped with pronounced horizontal striations and topped with a broadly triangular style base.

SPECIMENS EXAMINED. **Barbados.** ST. ANDREW: Turner's Hall, open pasture near woods, Sep 1940, *Gooding 433* (BAR); pasture off of highway (H2) between Baxters and Springvale, 11 Sep 1996, *Rogers 96-45* (BAR, MICH). ST. JOSEPH: Near Bloomsbury, site saturated with water, swampy, muddy, in cow pasture, 4 Nov 1996, *McClain 96-12* (BAR). ST. THOMAS: Harrison Cave, pasture, 6 Jun 1990, *Carrington & Taylor 1231* (BAR); Highland Gully, Jul 1937, *McIntosh 433* (BAR).

This abundant short-statured species inhabits pastures and similar moist, sunny places as well as the floors of some gullies. It is unique in having bright white "pseudopetals" or bracts with white markings. The species ranges widely in the New World tropics. Koyama (1979) recognized *Rhynchospora nervosa* subsp. *ciliata* (Vahl) T. Koyama, with short stolon-free rhizomes, leaves 2-4 mm wide (vs. 1-2 mm in subsp. *nervosa*) and sometimes longer than the culm (vs. as long as the culm or shorter). Barbados material conforms with subsp. *ciliata*.

Scleria Bergius, Kongl. Vetensk. Akad. Nya Handl. 26: 142, pl. 4,5. 1765.

Leaves borne on the culm; *flowers* unisexual, and *spikelets* usually monoecious; *carpellate flower* with the ovary usually above a "*hypogynium*"; *styles* 3; *achene* bony and remaining atop the hypogynium at dehiscence (hypogynium absent in *Scleria lithosperma*). About 200 species, mostly tropical.

25. **Scleria lithosperma** (L.) Sw., Prodr. 18. 1788. FLA 3: 315. Gooding et al., Fl. Barbados 82. Figure 37.

Delicate grasslike sedge with cauline leaves; *culm* 3-angled, to 40 (60) cm tall, slender, to 2 mm wide at the base, under 1 mm diam. apically; *leaves* linear, flexuous, up to 22 cm long × 2.5 mm wide, scabrous-margined; *inflorescences* terminal and axillary, to 5 cm long × 1 cm wide, spicate or scarcely paniculate, subtended by cauline leaves and having linear bracts resembling foliage leaves at the first-order inflorescence; *scales* ca. 5 mm long, narrowly lanceolate with hyaline margins and a thick midrib, this protruding apically as a short awn; *stamen* 1; *achenes* white.

SPECIMENS EXAMINED. **Barbados.** ST. JAMES: Gully side in shade, Plum Tree Gully, 2 Dec 1989, *Carrington 1111* (BAR); talus slope of gully, Plum Tree Gully, 11 Apr 1989, *Carrington & Taylor 978* (BAR). ST. JOSEPH: Foster Hall Woods, floor of semi-dry woodland, Sep 1940, *Gooding 378b* (BAR); rocky talus in rather dry forest, Foster Hall Wood, Jul 1940, *Gooding* [number illegible] (BAR). ST. PETER: Cherry Tree Hill, shaded forest floor near St. Nicholas Abbey, 17 Dec 1997, *Rogers 97-66* (BAR). ST. PHILIP: Top of ledge (S side) of gully in Three Houses Park, rocky, shaded, abundant, 9 Oct 1997, *Rogers 97-44* (BAR).

Scleria lithosperma is a small, delicate sedge of shaded, dry, rocky sites, such as the sides of gullies. It is compared with the far more common and much larger *S. melaleuca* under that species. *Scleria lithosperma* occurs worldwide in the tropics.

26. **Scleria melaleuca** Reichenb. ex Schlecht. & Chamisso, Lin-

naea 6: 29. 1831. Gooding et al., Fl. Barbados 83. Figure 38.

Scleria pterota Presl in Oken Isis 21: 268. 1826, *nomen nudum*. FLA 3: 310.

Robust rhizomatous sedge with leafy *culms* to ca. 50 (80) cm tall and 5 mm diam., the angled corners scabrous; *leaves* to 53 cm long × 15 mm wide with scabrous margins, plicate with 2 prominent nerves flanking the midvein, the apices long-acuminate; *inflorescences* terminal and lateral, up to 11 cm long × 4 cm wide, paniculate (orders of branching up to 3 [4], including the pedicels), subtended by cauline leaves, and with small linear-lanceolate bracts subtending the major axes; *flowers* in intermixed staminate and pistillate spikelets, the pistillate spikelets on the older, more central axes in quasi-dichasial clusters and the staminate spikelets tending to be more numerous and lateral; *staminate spikelets* resembling tiny ears of corn with many ligulate to lanceolate bracteoles tightly clustered around an apically protruding tuft of stamens, the basal scales sterile, the distal scales each subtending a single stamen; *pistillate spikelets* of similar shape and size, having fewer scales, the basal scales becoming large and protective in fruit; pistillate flower solitary, with its 3 *styles* protruding from the bract cluster; *achenes* globose, white, clasped basally by short, thickened lobes of the *hypogynium*.

SPECIMENS EXAMINED. **Barbados.** ST. ANDREW: Chalky Mt., 8 Aug 1904, *Murphy 459* (BAR); Turner's Hall Wood, 4 Oct 1937, *McIntosh & Allan 378ab* (BAR) [The collection *Gooding 378b* is *S. lithosperma*]. ST. JOSEPH: Pasture, Maynards, Jan 1936, *Mayers 378* (BAR); hilltop meadow near Sturges, Highway 3A, 6 Sep 1996, *Rogers 96-41* (BAR, MICH). ST. THOMAS: Coles Cave Gully, damp spot on gully floor, Jan 1940, *Gooding 378* (BAR). Parish unclear: Rocky pasture above Mt. Wilton Gully, 4 May 1937, *McIntosh 378a* (BAR).

Scleria melaleuca is common and widespread, and tends to be weedy. Habitats are variable: pastures, gully floors, marshy places, and scrubby waste areas. It and *S. lithosperma* are the only two Barbados sedges with cauline leaves and monoecious flowers; *Cyperus compressus* has low cauline leaves but perfect flowers. The uncommon *S. lithosperma* differs by having much narrower leaves (up to 2.5 mm as opposed to generally well over 5 mm wide). *Scleria melaleuca* occurs in the West Indies and South America.

Torulinium Desvaux in Hamilton, Prodr. 15. 1825.

Spikelets with distichous *scales; rachillae* breaking apart into units corresponding to single achenes, rachillae axes becoming corky-winged, the wings clasping the achene. Approximately 10 species, mostly in the Neotropics. The continued recognition of *Torulinium* by botanists who study Cyperaceae is in doubt, as the genus is not strongly differentiated from *Cyperus*. Authors merging the two include Correll and Correll (1982), Proctor (1984), and McVaugh (1993).

27. **Torulinium filiforme** (Sw.) C. B. Clarke in Urban, Symb. Antill 2 (1): 57. 1900. FLA 3: 288. Figure 39.

Cyperus filiformis Sw., Prodr. 20. 1788.

Thin, delicate sedge 18 cm tall; *culm* 1 mm diam.; *leaves* grasslike, some as tall as the culm, 1 mm wide; *inflorescence* pseudolateral, overtopped by a bract extending the line of the culm; additional bracts smaller; *spikelets* 2–5 in fingerlike clusters, up to 8–15 mm long; *scales* 3–7 per spikelet, spirally arranged and acute, ending in a point, tending to remain broad in upper half toward the apex.

This modest, inconspicuous sedge is known in Barbados from only one collection [ST. MICHAEL: Bridgetown, weed of lawn, Barbados Museum, 12 Apr 1989, *Carrington 1116* (BAR)] and had not been reported for Barbados previously. Searching the site and environs on multiple occasions failed to turn it up in 1997. It is distinctive by its extremely thin, grasslike nature. *Kyllinga brevifolia* is similar in this regard but has slightly broader leaves and consistently three bracts subtending its burrlike inflorescence (vs. up to 5 spikelets in a digitate cluster). *Torulinium filiforme* occurs in southern Florida and the West Indies.

28. **Torulinium odoratum** (L.) Hooper, Kew Bull. 26: 579. 1972. FLA 3: 287. Figure 40.

Cyperus odoratus L., Sp. Pl. 46. 1753. Gooding et al., Fl. Barbados, 77.

Large, robust sedge, the base slightly swollen with sometimes conspicuous adventitious roots; *culm* 30–80 cm tall, 3 mm diam. near the apex, triangular, smooth, topped with ca. 6–9 substantial leafy *bracts* up to 30 cm long × 12 mm wide; *leaves* often longer than the culm, up to 70 cm long × 12 mm wide, the sheaths purplish-brown; *inflorescence* ample, compound, 5–20 cm wide (excluding the bracts) and 20 cm tall; *rays* 5–7 in number, stiffly upright, up to 15 (20) cm long; *raylets* to 5 cm long; *spikelets* uncrowded and inserted at 90 degrees to the axis of the ray or raylet, (10) 15–25 mm long, yellow-green or yellow-brown at maturity; *scales* 8–16 in number, 2–3.5 mm long, translucent along borders, keeled; *stamens* 3; *styles* 3; *achene* ovate.

SPECIMENS EXAMINED. **Barbados.** ST. ANDREW: Turner's Hall Woods, in sun along dirt road leading into woods, 17 Dec 1996, *Rogers 96-158* (BAR). ST. JOSEPH: On muddy substrate within cow pasture in area of Bloomsbury, 4 Nov 1996, *McClain 96-14* (BAR); same locality, 20 Sep 1996, *Rogers 96-69* (BAR, MICH). ST. PHILIP: Three Houses, side of stream, May 1940, *Gooding 573* (BAR). ST. THOMAS: Bloomsbury, swampy ground, 15 Feb 1990, *Carrington & Taylor 1175* (BAR).

A large sedge encountered frequently in sunny wet sites. *Torulinium odoratum* is recognized by its long, narrow, light yellowish-brown spikelets inserted in uncrowded fashion at right angles to the axis that bears them. The living plants have a slight yellowish or brownish coloration. The species is pantropical.

ACKNOWLEDGMENTS. Dr. C. Dennis Adams supplied a series of valuable suggestions based in part on his work on the Cyperaceae of nearby Trinidad and Tobago and he vetted the manuscript. Dr. George Proctor of the Puerto Rico Dept. of Natural Resources has been a source of advice and help, including by joining Rogers on two field outings in Barbados. Dr. Anton Reznicek of the University of Michigan helped with troublesome identifications. Dr. Gordon Tucker of Eastern Illinois University lent a hand via e-mail. Most of the work was carried out at the Barbados National Herbarium (BAR) at the University of the West Indies, which provided financial support. Gratitude is due to the University of Michigan Herbarium (MICH) and to the University of Florida Herbarium (FLAS) for hosting visits by Rogers. University of the West Indies biology student Sadee Forde helped with collections. Without student Karen Greenidge's astute powers of observation we might never have known *Cyperus ochraceus* to grow on Barbados. As this is written, the entire known population could almost be covered with a tablecloth.

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Figure 1. *Abildgaardia ovata (Carrington & Taylor 1209).*

Figures 2, 3. *Cyperus alopecuroides (Rogers 97-8).*

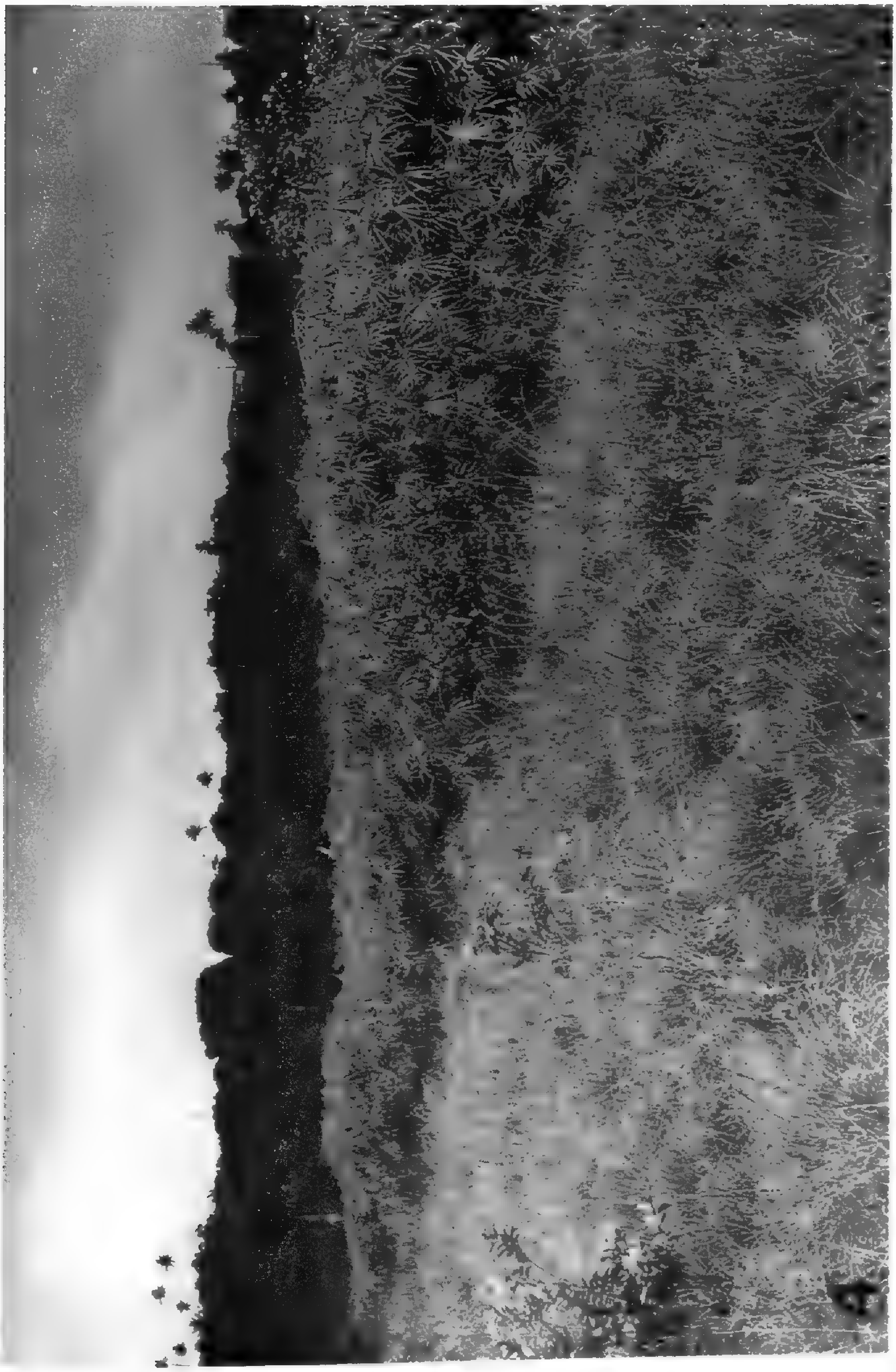

Figure 4. *Cyperus alternifolius* (*McClain 96-15*).

Figure 5. *Cyperus alternifolius (Rogers 97-14).*

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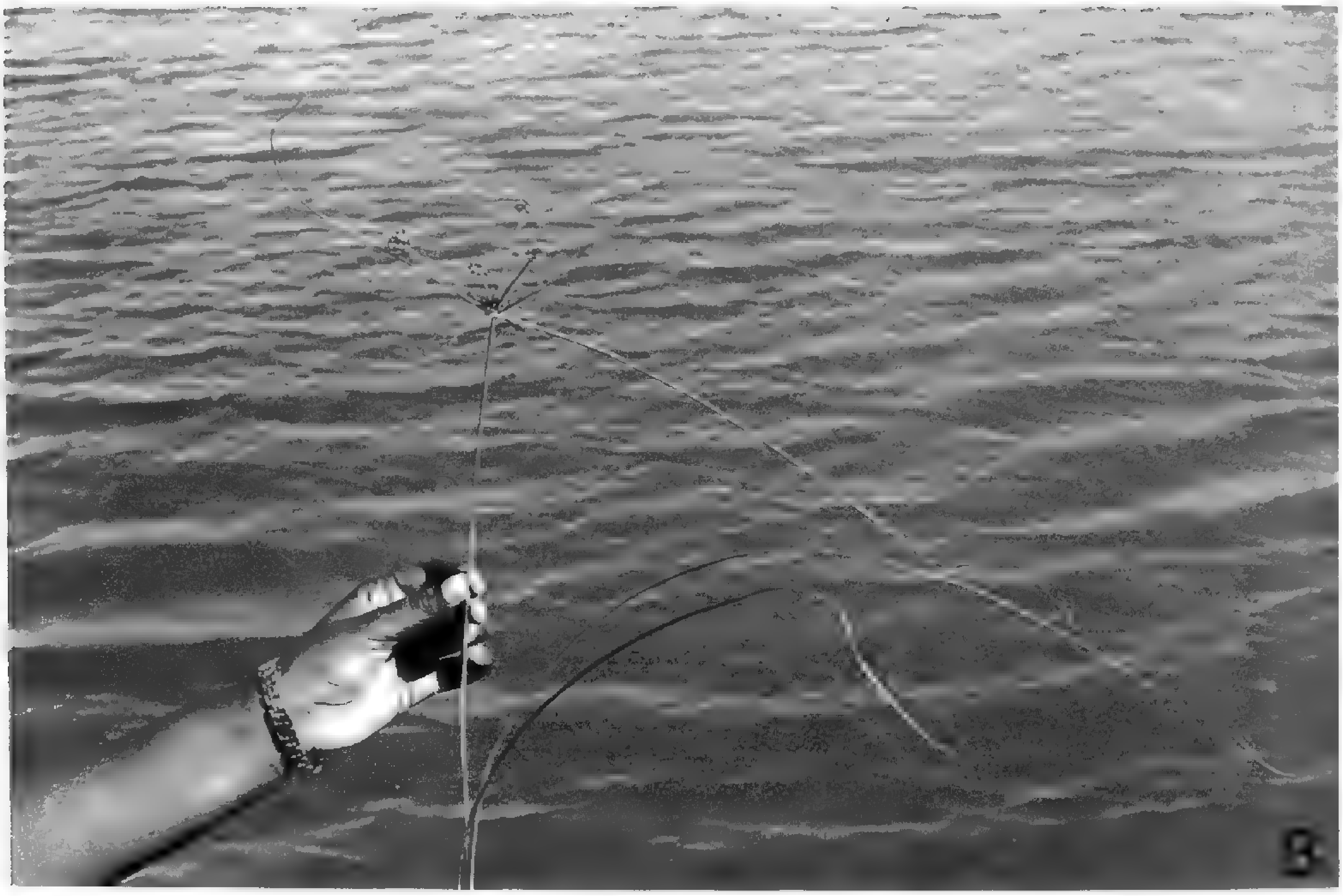
Figures 6, 7. *Cyperus compressus (Rogers 97-21).*



Figures 8, 9. *Cyperus elegans (Rogers 97-9).*

Figure 10. *Cyperus laevigatus (McIntosh 435-305a).*

Figures 11, 12. *Cyperus ligularis (Rogers 96-72, Forde 96-23).*

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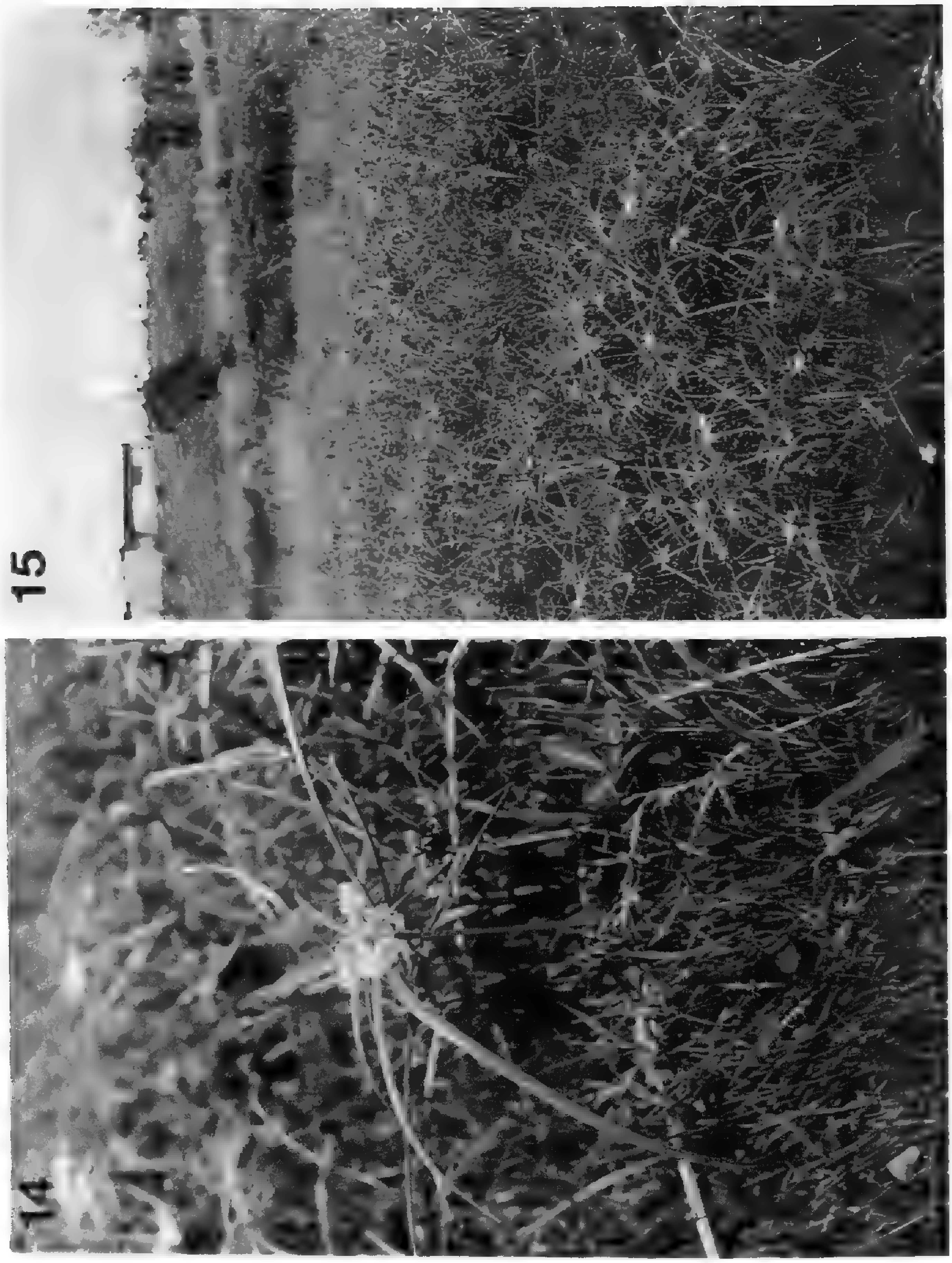
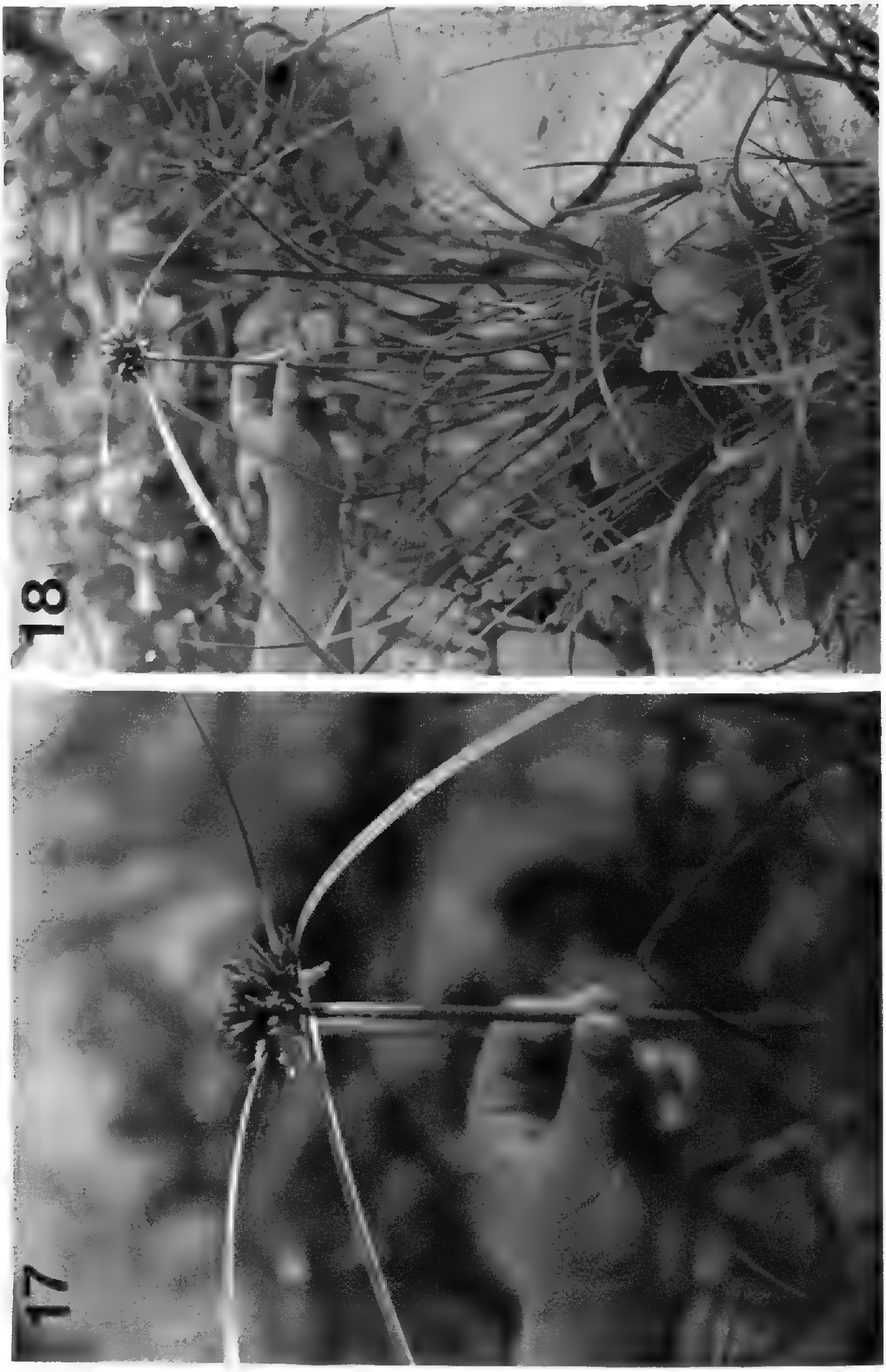
Figure 12. Continued. Figure 13. Rocky bluff at East Point, Barbados, with *Cyperus ligularis*.

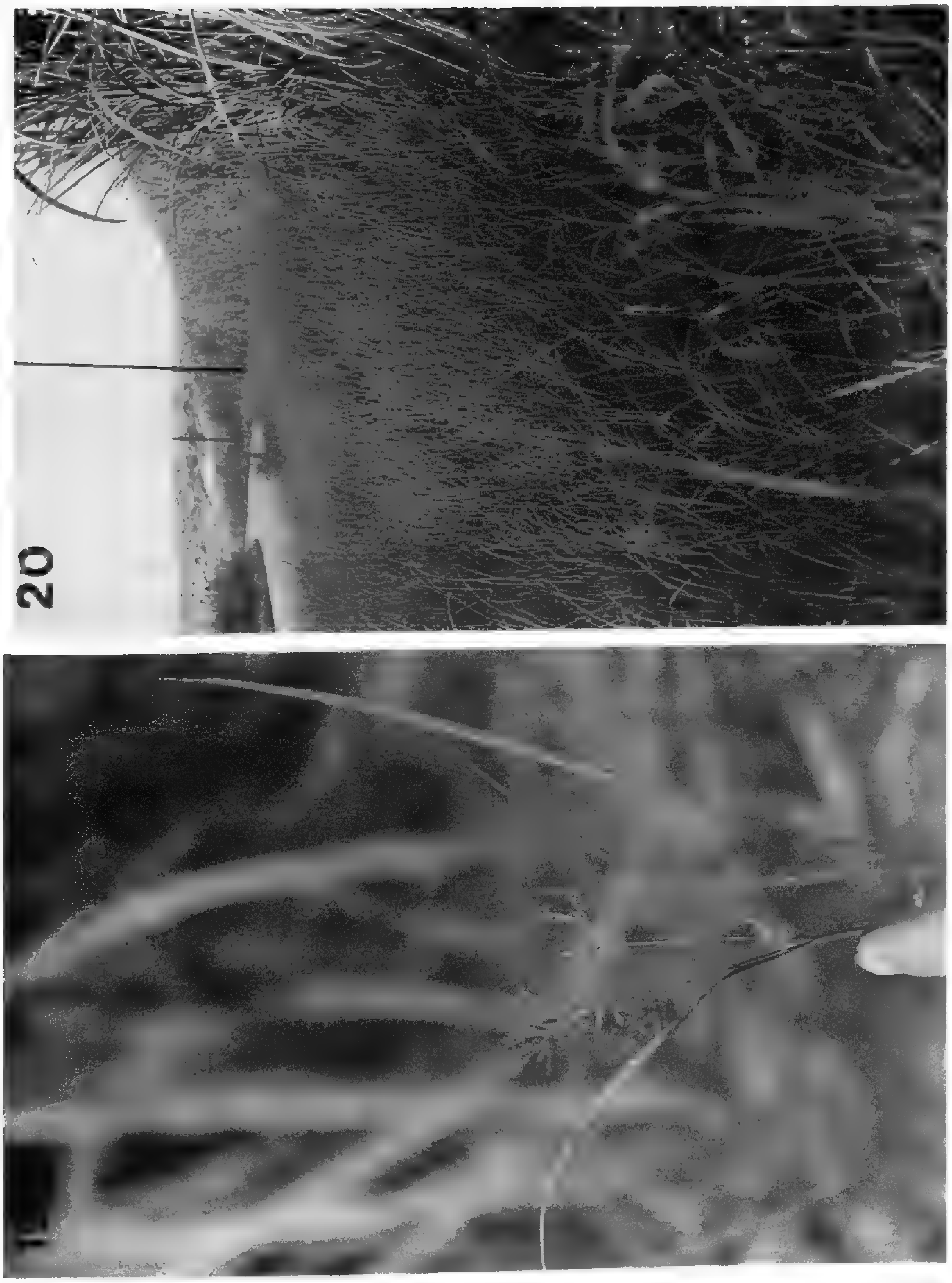


Figures 14, 15. *Cyperus luzulae* (*Rogers 96-50*).

Figure 16. *Cyperus ochraceus (Rogers 98-18).*



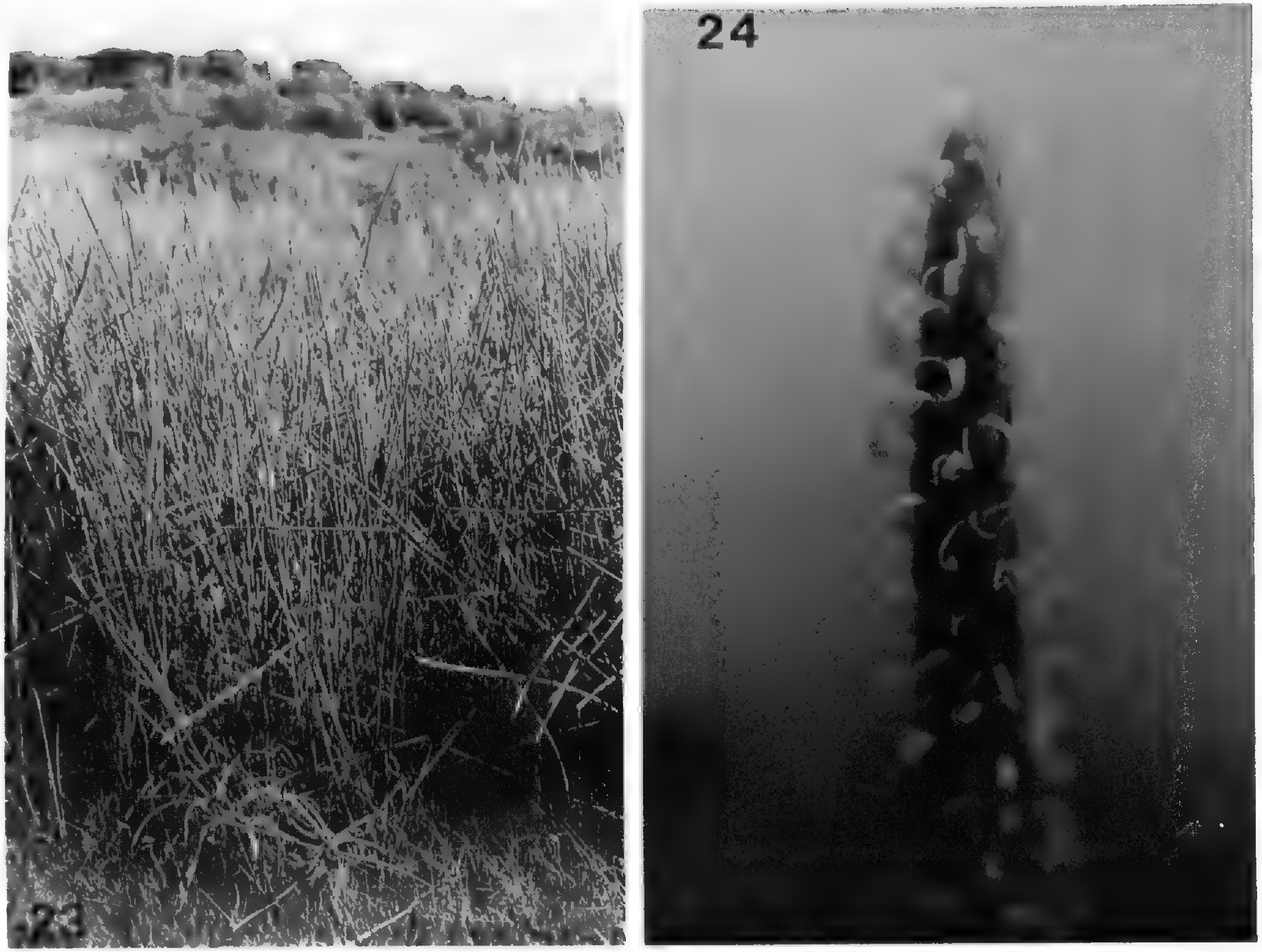
Figures 17, 18. *Cyperus planifolius (Rogers 96-73).*



Figures 19, 20. *Cyperus rotundus* (*Rogers 96-132*).

Figure 21. *Cyperus sphacelatus (Gooding 649).*

Figure 22. *Eleocharis geniculata* (Rogers 97-23).



Figures 23, 24. *Eleocharis interstincta (Rogers 96-49).*

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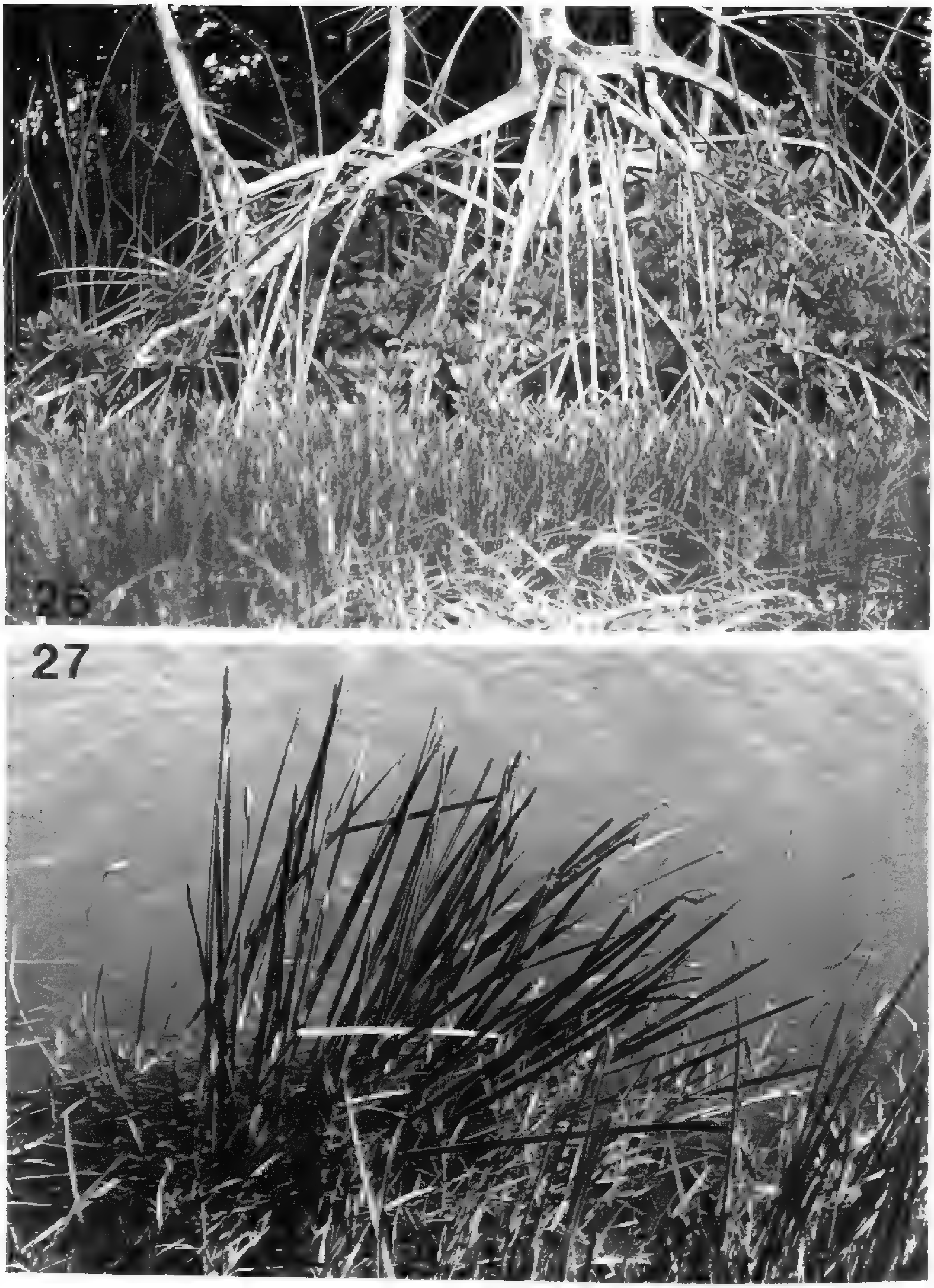
Figure 25. *Eleocharis macrostachya (Dept. Of Agriculture No. 545).*



Figures 26, 27. *Eleocharis mutata (Rogers 97-11).*

Figure 28. *Fimbristylis complanata (McClain 96-8).*

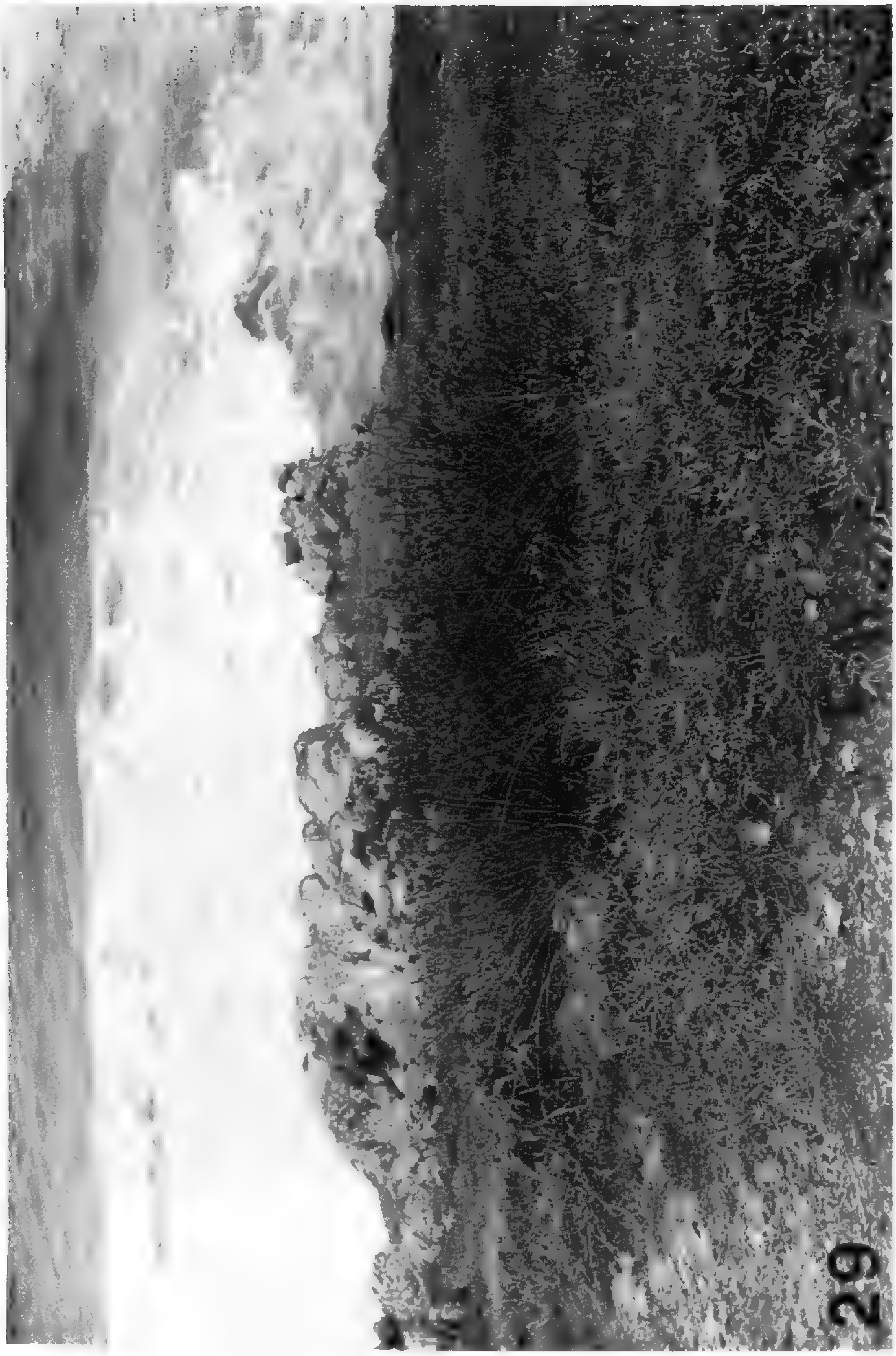


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Figure 29. *Fimbristylis cymosa* (*Rogers 96-65*).

Figure 30. *Fimbristylis dichotoma (McClain 96-10).*

Figures 31, 32. *Fimbristylis ferruginea (Rogers 96-129).*

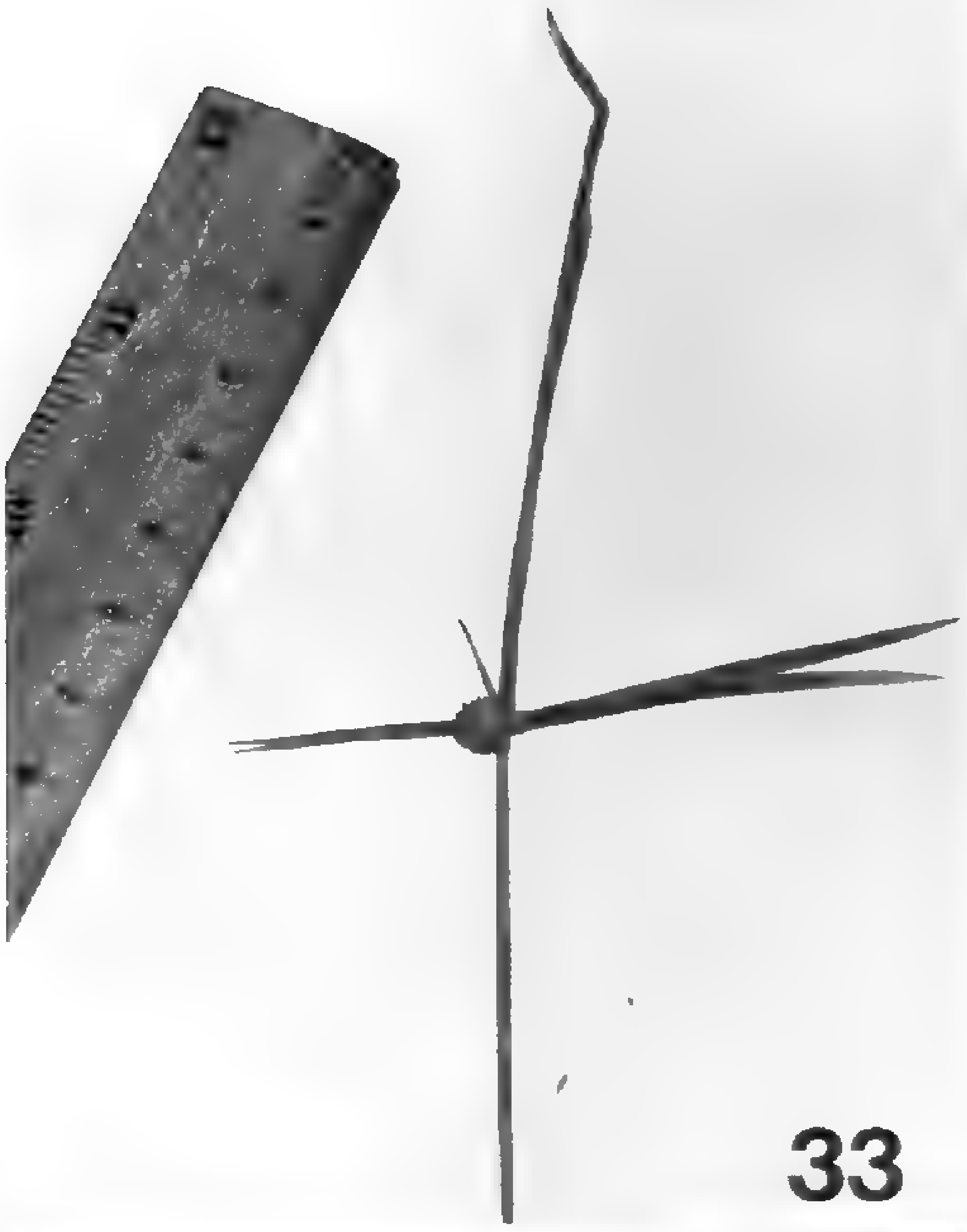

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Figure 33. *Kyllinga brevifolia (Carrington & Taylor 1176).* Figure 34. *Kyllinga nemoralis (Rogers 97-58).* Figure 35. *Pycreus polystachyos (Rogers 96-118).*

Figure 36. *Rhynchospora nervosa (McClain 96-12).*

Figure 37. *Scleria lithosperma* (*Gooding s.n. Jul 1940*). Figure 38. *Scleria melaleuca* (*McClain 96-9*).

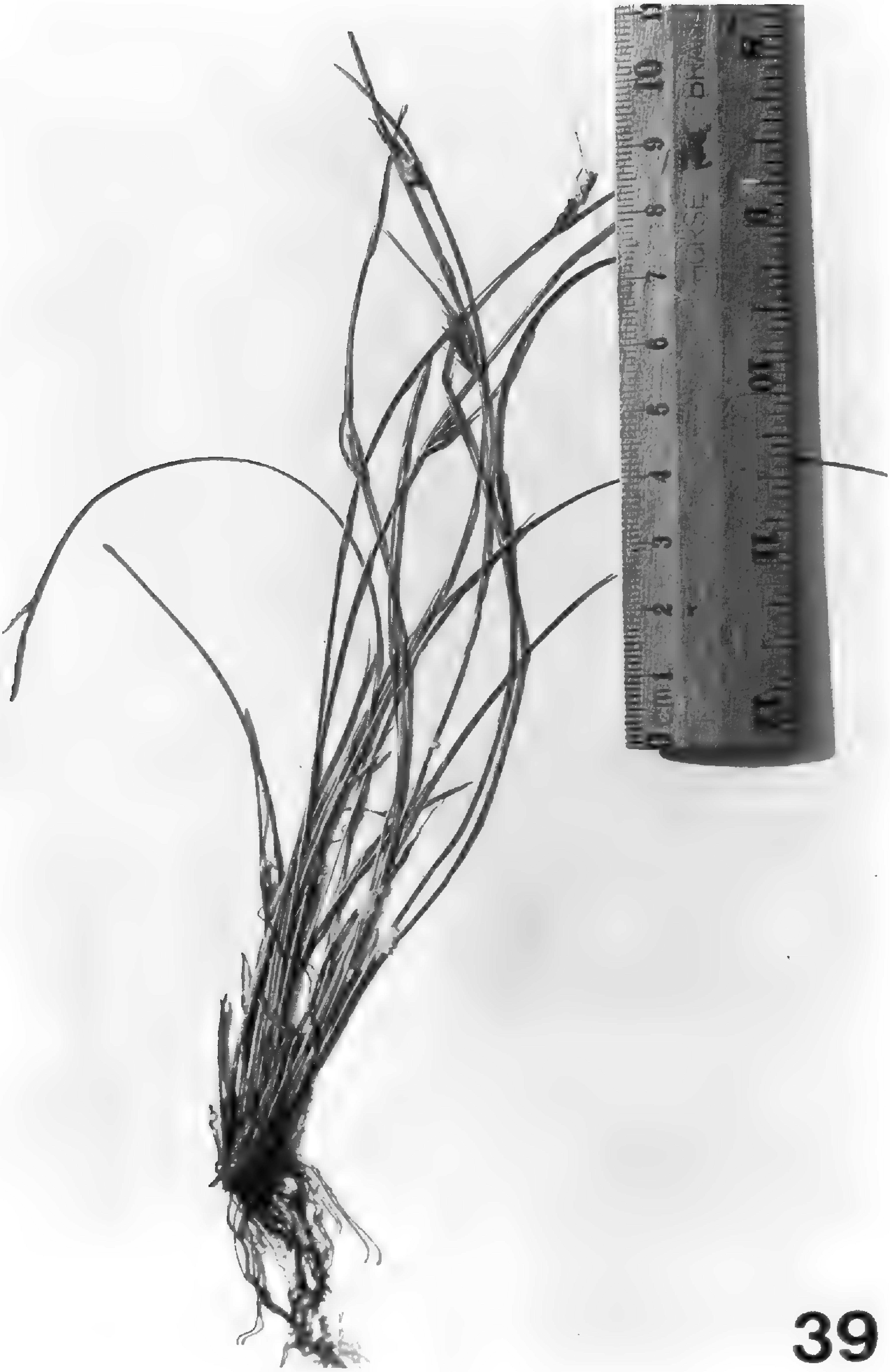

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Figure 39. *Torulinium filiforme (Carrington 1116).*

Figure 40. *Torulinium odoratum (McClain 96-14).*

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NEBC MEETING NEWS

September 1998. The away meeting featured a presentation by Dr. Rudolf Schuster on the topic "Age, Reproduction and Distribution of the Hepaticae: Problems of Being a Haploid." He was introduced by Dr. Karen Searcy who noted highlights of his career, including a Ph.D. from the University of Minnesota in 1948, a professorship at the University of Massachusetts from 1960–1983, and authorship of six volumes entitled *Hepaticae and Anthocerotae of North America, East of the Hundredth Meridian.* Karen also noted that the University of Massachusetts herbarium holds many of Dr. Schuster's specimens from Massachusetts and just received on indefinite loan from Mt. Holyoke College a bryophyte collection from A. J. Grout, author of *Mosses with a Hand-Lens and Microscope.*

Another title for Dr. Schuster's talk might have been "Hepatic Paradoxes." Threaded throughout his presentation were observations of evolutionary, biological, and distributional twists or peculiarities about liverworts. We learned, for instance, that the group, while being very old, has not been very successful evolutionarily relative to many younger plant groups. In support of this he compared the approximately 5000–7000 species described for the Hepaticae, which have existed since the Devonian, with the 25,000 species of orchids, a group that originated around the start of the Tertiary. He speculates that the primarily haploid existence of hepatics versus the predominantly diploid life history of higher plants has been one of the chief limiting factors for the former. In hepatics, the diploid matures its spores while they are still enveloped by haploid tissues; thus there is no direct selection pressure on the diploid generation, he explained. Being nonvascular, the gametophytes are limited in size. The sporophytes, being basically parasitic on these "incompetent" haploid generation plants, are likewise fixed in terms of potential size and growth.

Another paradox of the Hepaticae is that they are considered long-term survivors yet they are frequently unsuccessful at sexual reproduction. A major problem for many hepatics is that all or most of their disseminated spores result in unisexual or totally vegetative clones. Over 95% of primitive taxa, he says, are unisexual; thus a single isolated spore can produce only a clone capable of maintaining itself by asexual means. An example given by Schuster is *Acrobolbus ciliatus*, which exists as male populations in Japan and female populations in the Southern Appalachians. A converse corollary among hepatics, it might be stated, is that many species or populations which exist as isolated unisexual clones are successful reproducers and often persist for eons. How do they accomplish this? Mainly by a variety of asexual forms of reproduction. For instance, among the 350–400 "good" species of *Plagiochila*, all are unisexual and many are known from one sex only. The Appalachian taxa reproduce mainly by fragmenting (e.g., *P. caduciloba*) or caducous leaves (e.g., *P. austinii*), a seemingly lousy way to get around, Schuster says, but then adds "maybe such fragments adhere to squirrel feet." Such fun thinking helped get us out of our anthropocentric mind sets in thinking about successful strategies for these small plants. Besides asexual disseminules, including gemmae in some taxa, some hepatics have the strategy of pure persistence, existing as hardy clones for centuries or millenia. For instance, *P. corniculata*, we were told, is waiting for sperm from male plants in Europe to make it across the Atlantic to fertilize the female clones in America. The genus *Haplomitrium* has evolved what appears to be a better game for overcoming lives of being unisexual clones lacking any asexual means of reproducing. Its taxa reproduce only by spores shed as diads or tetrads, which guarantees that at least some of the germinating diads and all of the tetrads will have the potential of producing gametophytes of both sexes in close proximity, and, therefore, at least the possibility of self fertilization.

A distributional paradox about Hepaticae is that while being a very old group, they have failed to spread well. Evidently, infrequent spore production, short spore viability, and other limitations to dispersal have restricted many taxa geographically. Oddly, Schuster points out, hepatics are poorly represented in geologically old areas such as the Appalachians in spite of their ability to persist as clones. All three endemic hepatic genera in North America, Schuster says, occur in orogenically young westernmost areas. Likewise in South America, the geologically old Guayana shield area has yielded only 3–4 endemic genera compared to at least 10–12 for the northern Andes. A partial explanation Schuster gives for this is that hepatics are basically pioneer taxa. In orogenically unstable sites, he suggests, there is persistence of old taxa plus opportunity for evolution to occur in newly created raw and diverse habitats. In geologically old areas, he speculates there has been mass extinction of species through time plus a reduction of pioneer substrates where hepatics can easily grow and evolve.

—PAUL SOMERS, Recording Secretary

ANNOUNCEMENT

RHODORA CENTENNIAL SYMPOSIUM

This spring, the New England Botanical Club will host a symposium to celebrate the centennial of its publication, *Rhodora.* The symposium, entitled "The Dynamics of the New England Flora," will be held April 9–10, 1999, in Cambridge, Massachusetts. The talks will begin on Friday evening with an address by Dr. Peter H. Raven, Director of the Missouri Botanical Garden. On Saturday, speakers will include Dr. Warren H. Wagner of the University of Michigan and Dr. Bruce H. Tiffney of the University of California at Santa Barbara.

Additional information and registration form may be obtained at our web site (http://www.herbaria.harvard.edu/nebc/) or by writing to: The New England Botanical Club, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138.

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1997–1998

The Editor-in-Chief of *Rhodora* is grateful to the members of the editorial staff and to each of the following specialists for their participation in the review process. The conscientious and thorough review of manuscripts by the reviewers and staff helps to maintain the quality of this journal.

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ABSTRACT: An abstract and a list of key words should be included with each paper, except for shorter papers submitted as Notes. An abstract must be one paragraph, and should not include literature citations or taxonomic authorities. Please be concise, while including information about the paper's intent, materials and methods, results, and significance of findings.

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FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad

distribution. Keys and synonymy for systematic revisions should be prepared in the style of "A Monograph of the Genus *Malvastrum*," S. R. Hill, RHODORA 84: 159–264, 1982. Designation of a new taxon should carry a Latin diagnosis (rather than a full Latin description), which sets forth succinctly how the new taxon differs from its congeners.

LITERATURE CITED: All bibliographic entries must be cited in the paper, unless a special exception has been made by the Editor (such papers will be allowed a REFERENCES section). Verify all entries against original sources, paying special attention to spelling and details of publication. Cite references in strict alphabetical order by first author's surname. Do not write authors' names in all capital letters. References by a single author precede multi-authored works of same senior author, regardless of date. Use a long dash when the author(s) is the same as in the entry immediately preceding (see recent issues). Refer to Botanico-Periodicum-Huntianum (B-P-H 1968) and B-P-H/ Supplement (1991) for standardized abbreviations for journals.

TABLES: Tables must be double-spaced. Tables may be continued on an extra page, if necessary. As much as possible, the title should be self-explanatory. Do not use footnotes; instead, add notes after the end of the table title. Broadside tables should be avoided, if possible. Each table should be cited in the text in numerical order.

FIGURES: Illustrations must be either black and white half-tones (photographs), drawings, or graphs. Illustrations must be camera-ready; flaws cannot be corrected by the Editor or the printer. Add symbols or shading with press-on sheets. The printed plate will be 4 × 6 inches; be sure that illustrations are proportioned to reduce correctly. Allow space for a caption, if possible. Magnification/reduction values should be calculated to reflect the actual printed size. Maps must indicate scale and compass direction. The double-spaced list of legends for figures should be provided on a separate page. Each figure should be cited in the text in numerical order.

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22 Divinity Avenue
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The New England Botanical Club is a nonprofit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, and has a large herbarium of New England plants and a library. It publishes a quarterly journal, RHODORA, which is now in its 100th year and contains about 400 pages per volume. Visit our web site at http://www.herbaria.harvard.edu/nebc/

Membership is open to all persons interested in systematics and field botany. Annual dues are $35.00, including a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

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INDEX TO VOLUME 100

New scientific names are in bold face.

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